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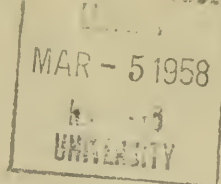
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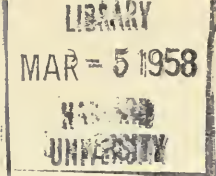
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THE UNIVERSITY OF KANSAS SCIENCE BULLETIN

VOL. XXXVIII, PT. II] MARCH 20, 1958

[No. 13

Contribution to the Herpetology of Thailand

BY

EDWARD H. TAYLOR ¹ and ROBERT E. ELBEL ²

ABSTRACT. A collection of Amphibia and Reptiles from Thailand is reviewed. The following forms are regarded as new: *Micrixalus magnapustulosus*, *Mabuya macularia postnasalis*, *Mabuya macularia quadrifasciata*, *Mabuya macularia malcolmi*, *Leiopisma siamensis*, *Sibynophis collaris triangularis* and *Parahelicops boonsongi*.

The known herpetological fauna of Thailand is listed as follows: Salamanders 1, caecilians 2, frogs and toads 76, turtles 24, crocodiles 2, lizards 86, and snakes 130, with a grand total of 321 species and subspecies.

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INTRODUCTION

In the years 1953 and 1954 the senior author identified the species in certain collections of reptiles and amphibia sent to him from Thailand through the U. S. State Department. With the exception of a few duplicate specimens the collections were returned to Thailand, the specimens retained being placed in the Museum of the University of Kansas. These collections, brought together largely through the efforts of Dr. Boonsong Lekagul and the junior author, will eventually become the basis of a national Thai collection. In 1955 the junior author, who had spent the preceding four years in Thailand with the United States Operations Mission to Thailand, returned to the United States with a number of specimens which are now incorporated in the EHT-HMS Collection, property of the senior author.

This latter collection also contains considerable studied material from Thailand. One part of this was collected by Baron de Schauensee and was reported by the senior author, in 1934.* Another part was obtained by exchange with Dr. Malcolm Smith, long resident of Thailand and physician to his Majesty the King of Siam (now Thailand). Some of these are cotypes, paratypes or topotypes, all identified by Dr. Smith.† These have been of especial help in the study of our collections.

* Proceedings of the Academy of Natural Sciences, Philadelphia, vol. 86, 1934, pp. 281-310, pls. 17, text figs., 1-4.

† In describing new forms Dr. Smith frequently designated a small series of numbers as the "type series" although he may have had numerous other specimens before him.

A third collection, from French Indo-China, obtained by exchange through the kindness of Dr. René Bourret of the Institut Oceanographique de l'Indochine, has been indeed valuable for comparative study.

The country of Thailand is a strategic area in the study of the south Asian faunae since its southern peninsula represents the highway along which emigrants from the continent reached the territories of the East Indies and the Philippines; and at the same time species from the latter areas reached the peninsula and the mainland. While it is not always certain in which direction the movement took place, on the basis of the known distribution of a species, it is possible to postulate its place of origin and later movement. Thus it becomes evident that tracing the distribution of species throughout Thailand can yield information of broad interest. Moreover the mainland part of Thailand, especially the northern part, is in a measure the pathway of exchange between Burma and the Chinese—Indo-Chinese territories and thus the distributional data lends much to our understanding of the faunae of these territories.

ACKNOWLEDGMENTS

We wish to express our thanks to Dr. Boonsong Lekagul of Thailand who was instrumental in collecting or acquiring much of the material from Thailand; to Mr. John Legler, curator in charge of the herpetological collections of the University of Kansas, who has been most helpful in making available materials and specimens in his charge; to Mr. H. G. Deignan, U. S. National Museum for help in clarifying certain locality designations. We especially acknowledge use of the published works of Dr. Malcolm Smith treating of the faunae of Thailand and Southeastern Asia.

METHODS

In this paper we are listing Thai species in the University collections (designated by the letters KUMNH) and certain ones in the private collection of the senior author (designated EHT-HMS). No attempt has been made to give all literature references and synonyms, nor have we attempted to give all Thai localities in which specimens have been taken. The names Siam and Thailand are interchangeable. Siam appears in the older literature, Thailand in the more recent. However, on postage stamps of the country one or the other name appears at this time (1956).

Concerning the field numbers, the early RE and Y numbers were collected by Robert E. Elbel except for RE 1300 to RE 1556 and

RE 2000 to RE 2500 which were collected by Robert E. Elbel and H. G. Deignan; the numbers RE 3000 to RE 3975 were collected by Robert E. Elbel and Dr. Boonsong Lekagul; the numbers above RE 3975 were collected by Robert E. Elbel; all other field numbers were collected by Dr. Boonsong Lekagul.

As for the spelling of Thai names, we are using the scheme of transliteration from the Thai alphabet adopted by the Thai Government nearly two decades ago, and likewise used in the U. S. Army Gazetteer of 1944. This is often at variance with spellings encountered in European or older American maps, or in other reports. We feel that an effort should be made to stabilize the system of transliteration.

HISTORICAL REVIEW

A considerable amount of collecting has already been done in Thailand and numerous reports have appeared as evidenced by the bibliography. No effort has been made to make the list complete. Many of the older works, in which references to specimens from Siam are made, are omitted.

Among the most important works on the herpetological fauna of Thailand are those of Dr. Malcolm Smith, especially his volumes on the Reptilia and Amphibia in "The Fauna of British India" and the "Reptilia and Amphibia of the Malay peninsula from the Isthmus of Kra to Singapore." Numerous shorter papers of his, dealing with the Thai reptiles and amphibians, have appeared in various journals.

The snake, lizard and batrachian catalogues of the British Museum by George A. Boulenger are indispensable in a study such as this.

Two papers by Major Stanley Flower are "Notes on a collection of Reptiles and Batrachians made in the Malay Peninsula in 1895-96", and "Notes on a second collection of reptiles made in the Malay Peninsula and Siam." These two with a similar paper on the Batrachians constitute a major contribution.

In the report at hand the locality records of many specimens collected by the junior author are pin-pointed by recording the name of the subvillage, village, district, and province, and where a particular mountain is involved this is given with the approximate elevation. Since most maps of Thailand fail to show the 71 provinces, a chart is presented showing the location of each. Often a village, a district, and province may have the same name and in older records it is not always possible to determine which is intended.

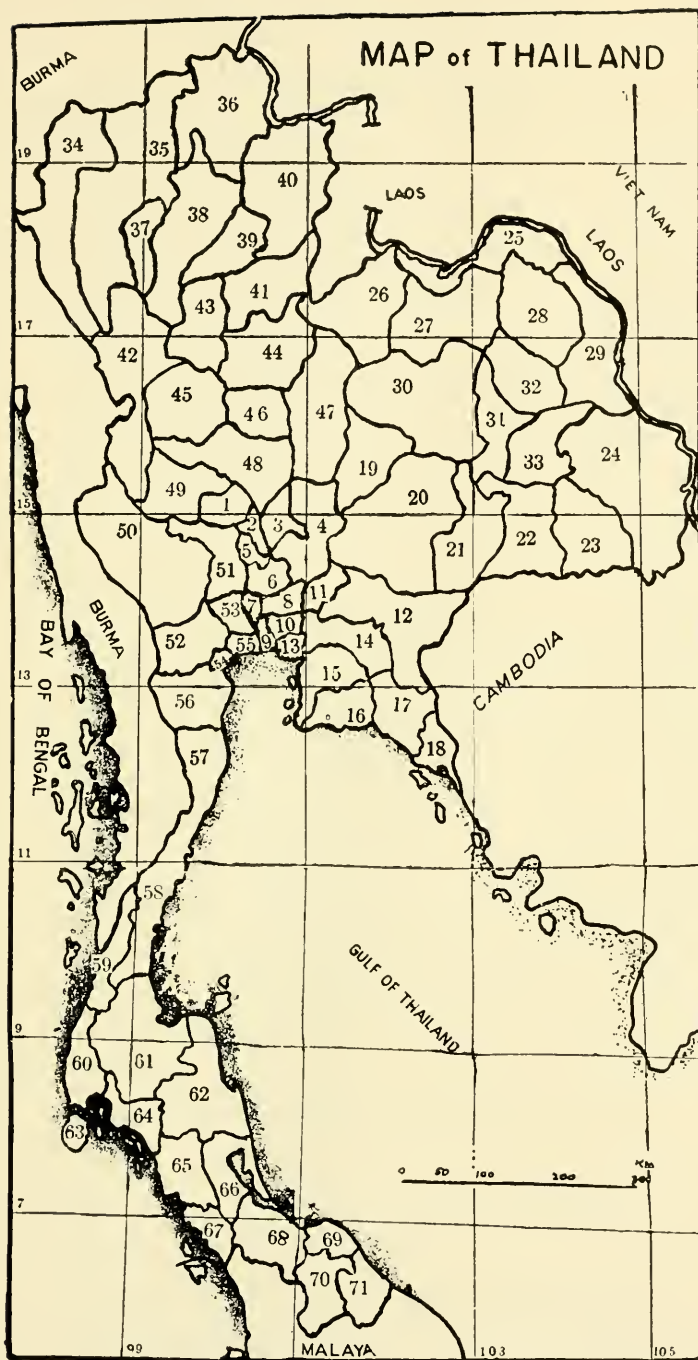


FIG. 1. Map of Thailand. (The numbers refer to names of provinces and in themselves have no significance.)

LIST OF THAI PROVINCES

Corrected spellings as used by the U. S. Army Gazetteer, 1944.

- | | |
|--------------------------------|-------------------------|
| 1. Chainat | 37. Lamphun |
| 2. Sing Buri | 38. Lampang |
| 3. Lop Buri | 39. Phrae |
| 4. Sara Buri | 40. Nan |
| 5. Ang Thong | 41. Uttaradit |
| 6. Ayutthaya | 42. Tak |
| 7. Nonthaburi | 43. Sukhothai |
| 8. Pathum Thani | 44. Phitsanulok |
| 9. Thon Buri | 45. Kamphaeng Phet |
| 10. Phra Nakhon (Bangkok) | 46. Phichit |
| 11. Nakhon Nayok | 47. Phetchabun |
| 12. Prachin Buri | 48. Nakhon Sawan |
| 13. Samut Prakan | 49. Uthai Thani |
| 14. Chachoengsao | 50. Kanchanaburi |
| 15. Chon Buri | 51. Suphan Buri |
| 16. Rayong | 52. Rat Buri |
| 17. Chanthaburi | 53. Nakhon Pathom |
| 18. Trat | 54. Samut Songkhram |
| 19. Chaiyaphum | 55. Samut Sakhon |
| 20. Nakhon Ratchasima (Khorat) | 56. Phet Buri |
| 21. Buriram | 57. Prachuap Khiri Khan |
| 22. Surin | 58. Chumphon |
| 23. Khu Khan (Sisaket) | 59. Ranong |
| 24. Ubon | 60. Phangnga |
| 25. Nong Khai | 61. Surat Thani |
| 26. Loei | 62. Nakhon Si Thammarat |
| 27. Udon Thani | 63. Phuket |
| 28. Sakon Nakhon | 64. Krabi |
| 29. Nakhon Phanom | 65. Trang |
| 30. Khon Kaen | 66. Phatthalung |
| 31. Maha Sarakham | 67. Satun |
| 32. Kalasin | 68. Songkhla |
| 33. Roi Et | 69. Pattani |
| 34. Mae Hong Son | 70. Yala |
| 35. Chiang Mai | 71. Narathiwat |
| 36. Chiang Rai | |

A LIST OF THE AMPHIBIANS KNOWN FROM THAILAND *

CAUDATA

SALAMANDRIDAE

Tylototriton verrucosus Anderson

GYMNOPHIONA

CAECILIIDAE

**Ichthyophis glutinosus* (Linnaeus)*Ichthyophis monochrous* (Bleeker)

* The asterisk in front of a name indicates that the species is treated herein.

SALIENTIA

PELOBATIDAE

- Megophrys nasuta (Schlegel)
- Megophrys longipes (Boulenger)
- *Megophrys aceras (Boulenger)
- Megophrys feae (Boulenger)
- Megophrys monticola (Günther)
- Megophrys pelodytoides (Boulenger)
- *Megophrys hasselti hasselti (Tschudi)

BUFONIDAE

- *Bufo asper Gravenhorst
- Bufo borbonica (Kühl and van Hasselt)
- Bufo macrotis Boulenger
- *Bufo melanostictus Schneider
- Bufo parvus Boulenger
- Bufo penangensis Stoliczka
- Nectophryne hosii Boulenger

HYLIDAE

- Hyla annectens (Jerdon)

RANIDAE

- *Ooeidozyga lima Kühl and van Hasselt
- *Phrynoglossus laevis martensi (Peters)
- Elachyglossa gyldenstolpi Andersson
- Rana cyanophlyctis Schneider
- *Rana tigerina pantherina Fitzinger [= *Rana rugulosa* Wiegmann]
- Rana cancrivora cancrivora Gravenhorst
- Rana cancrivora raja M. Smith
- *Rana limnocharis limnocharis Boie *in* Wiegmann
- Rana macrodon Kühl
- Rana kochangae M. Smith
- Rana doriae Boulenger
- Rana pileata Boulenger
- *Rana macrognatha macrognatha Boulenger
- Rana hascheana (Stoliczka) [= *Rana limborgi* Sclater *fide* M. Smith]
- Rana aenea M. Smith
- *Rana kuhlii Schlegel *in* Duméril and Bibron
- Rana laticeps Boulenger
- Rana mortenseni Boulenger
- *Rana cubitalis M. Smith
- *Rana nigrovittata (Blyth)
- Rana humeralis Boulenger
- Rana niopus Boulenger
- Rana macrodactyla (Günther)
- Rana nicobariensis (Stoliczka)
- Rana alticola Boulenger
- *Rana erythraea (Schlegel)
- Rana scutigera Andersson
- Rana signata (Günther)
- Rana tasanae M. Smith

- Rana glandulosa* Boulenger
Rana luctuosa (Peters)
Rana haasei M. Smith
 **Rana chalconota* (Schlegel)
 **Micrixalus magnapustulosus* sp. nov.
Micrixalus tenasserimensis (Sclater)

RHACOPHORIDAE

- **Rhacophorus leucomystax leucomystax* (Gravenhorst)
Rhacophorus nigropalmatus Boulenger
Rhacophorus prominans M. Smith
Rhacophorus colletti Boulenger
Rhacophorus bimaculatus Boulenger
Philautus asper (Boulenger)
Philautus horridus (Boulenger)
Philautus vittatus (Boulenger)
Philautus petersi (Boulenger)
Philautus pictus (Boulenger)
Philautus bimaculatus (Peters)
Chirixalus doriae Boulenger

MICROHYLIDAE

- Microhyla pulchra* (Hallowell)
Microhyla inornata Boulenger
Microhyla ornata (Duméril and Bibron)
Microhyla annamensis M. Smith
Microhyla butleri Boulenger
Microhyla heymonsi Vogt
Microhyla annectens Boulenger
 **Microhyla berdmorei* (Blyth)
Kalophrynus pleurostigma (Müller)
Kaloula mediolineata M. Smith
 **Kaloula pulchra pulchra* Gray
 **Glyphoglossus molossus* Günther
Calluella guttulata (Blyth)

A LIST OF THE REPTILIA KNOWN FROM THAILAND

TESTUDINES

DERMOCHELIDAE

- Dermochelys coriacea* (Linnaeus)

CHELONIIDAE

- Eretmochelys imbricata* (Linnaeus)
Chelonia mydas (Linnaeus)
Lepidochelys olivacea (Eschscholtz)

PLATYSTERNIDAE

- **Platysternon megacephalum* Gray

EMYDIDAE

- ?*Cyclemys mouhotii* Gray
Cyclemys dentata (Gray)
Cuora amboinensis (Daudin)
 ?*Geoemyda spengleri* (Gmelin)
Geoemyda spinosa (Bell in Gray)

Geoemyda trijuga edeniana (Theobald)
Geoemyda grandis Gray
Damonia ** *subtrijuga* (Schlegel and S. Müller)
Hieremys annandalii (Boulenger)
Notochelys platynota (Gray)
Siebenrockiella crassicolis (Gray)
Batagur baska (Gray)

TESTUDINIDAE

Testudo elongata Blyth
Testudo emys Schlegel and S. Müller
Testudo impressa (Günther)

TRIONYCHIDAE

Pelochelys bibroni (Owen)
Chitra indica (Gray)
Dogania subplana (Geffroy-St. Hilaire)
Amyda cartilaginea (Boddaert)

CROCODYLIA

CROCODYLIDAE

**Crocodylus siamensis* Schneider
Crocodylus porosus Schneider

A LIST OF THE REPTILES KNOWN FROM THAILAND

SAURIA

GEKKONIDAE

**Cyrtodactylus intermedius* (Smith)
Cyrtodactylus consobrinoides (Annandale)
Cyrtodactylus oldhami (Theobald)
Cyrtodactylus peguensis (Boulenger)
Cyrtodactylus angularis (Smith)
Cyrtodactylus brevipalmatus (Smith)
Cnemaspis siamensis (Smith)
Cnemaspis affinis (Stoliczka)
Aleuroscalabotes felinus (Günther)
Phyllodactylus siamensis Boulenger
**Hemidactylus frenatus* Schlegel (in Duméril and Bibron)
Hemidactylus garnoti Duméril and Bibron
**Cosymbotus platyurus* (Schneider)
Cosymbotus craspedotus (Mocquard)?
**Peropus mutilatus* Wiegmann
Hemiphyllodactylus typus typus Bleeker
**Gekko gekko* (Linnaeus)
Gekko smithii Gray
Ptychozoon lionatum Annandale
Ptychozoon kuhli Stejneger

AGAMIDAE

**Draco whiteheadi* Boulenger
**Draco maculatus* (Gray)
**Draco haasei* Boettger

** Mertens and Wermuth (Zool. Jahrb., Band 85, Heft 5, 1955) use the name *Malayemys* Lindholm, 1931.

- **Draco blanfordi* Boulenger
- Draco divergens* Taylor
- Draco volans* Linnaeus
- Draco fimbriatus* Kuhl
- Draco punctatus* Boulenger
- Draco cyanolaemus* Boulenger
- Draco taeniopterus* Günther
- Draco formosus* Boulenger
- **Draco melanopogon* Boulenger
- Draco microlepis* Boulenger
- Draco quinquefasciatus* Gray
- **Goniocephalus armatus armatus* (Gray)
- **Goniocephalus armatus crucigerus* (Boulenger)
- Goniocephalus lepidogaster* (Cuvier)
- Goniocephalus doriae* Peters
- Goniocephalus abbotti* Cochran
- Calotes cristatellus* (Kuhl)
- **Calotes floweri* Boulenger
- **Calotes versicolor*. (Daudin)
- **Calotes emma* Gray
- **Calotes mystaceus* Duméril and Bibron
- **Liolepis belliana belliana* (Gray)
- **Physignathus cocincinus* Cuvier

VARANIDAE

- **Varanus bengalensis nebulosus* (Gray)
- Varanus rudicollis* (Gray)
- Varanus s. salvator* (Laurenti)
- Varanus d. dumerilii* (S. Müller *in* Schlegel)

LACERTIDAE

- Takydromus sexlineatus* Daudin

SCINCIDAE

- **Mabuya macularia postnasalis* subsp. nov.
- **Mabuya macularia quadrifasciata* subsp. nov.
- **Mabuya macularia malcolmi* subsp. nov.
- **Mabuya m. multifasciata* (Kuhl)
- **Mabuya longicaudata* (Hallowell)
- Mabuya praesigne* (Boulenger)
- Mabuya rugifera* (Stoliczka)
- **Eumeces quadrilineatus* (Blyth)
- **Dasia olivacea* Gray
- **Sphenomorphus indicus indicus* (Gray)
- Sphenomorphus tersus* (Smith)
- **Sphenomorphus maculatus* (Blyth)
- Lygosoma quadrupes* (Linnaeus)
- Siaphos quadrivittatum* (Peters)
- **Leiolopisma rupicola* (Smith)
- **Leiolopisma eunice* Cochran
- Leiolopisma reevesii reevesii* (Gray)
- Leiolopisma reevesi melanostictum* (Boulenger)
- Leiolopisma tavesae* Smith

- Leiopisma kohtaoensis* Cochran
- ?*Leiopisma doriae* (Boulenger)
- Leiopisma vittigerum vittigerum* (Boulenger)
- **Leiopisma siamensis* sp. nov.
- Riopa koratense* (Smith)
- Riopa bowringii* (Günther)
- Riopa isodactyla* (Günther)
- Riopa herberti* (Smith)
- Tropidophorus berdmorei* (Blyth)
- Tropidophorus robinsoni* Smith
- Tropidophorus thai* Smith
- Tropidophorus microlepis* Günther
- Ophioscincus anguinoides* (Boulenger)
- Ophioscincus roulei* (Angel)
- Ophioscincus gyldenstolpei* (Lönnberg)

DIBAMIDAE

- Dibamus novae-guineae* Duméril and Bibron

SERPENTES

TYPHLOPIDAE

- Typhlops braminus* (Daudin)
- Typhlops floweri* Boulenger
- Typhlops lineatus* Boie
- Typhlops albiceps* Boulenger
- **Typhlops diardi muelleri* Schlegel

ANILIIDAE

- Cylindrophis rufus rufus* (Laurenti)

XENOPELTIDAE

- Xenopeltis unicolor* Reinwardt *in* Boie

BOIDAE

- Python reticulatus* (Schneider)
- Python molurus bivittatus* Schlegel

DIPSADIDAE

- Pareas laevis* (Boie)
- Pareas malaccanus* (Peters)
- Pareas margaritophorus* (Jan)
- **Pareas carinatus* (Boie)
- Pareas hamptoni* (Boulenger)
- **Pareas macularius* Theobald
- Haplopeltura boa* (Boie)

COLUBRIDAE

Xenoderminae

- Xenodermus javanicus* Reinhardt

Sibynophiinae

- Sibynophis geminatus* (Boie)
- **Sibynophis collaris triangularis* subsp. nov.

Acrochordinae

- Acrochordus javanicus* Hornstedt
- **Acrochordus granulatus* (Schneider)

Colubrinae

- Gonyosoma oxycephalum (Boie)
- Elaphe flavolineata (Schlegel)
- Elaphe taeniura (Cope)
- *Elaphe radiata (Schlegel)
- Elaphe porphyracea porphyracea (Cantor)
- *Ptyas mucosus (Linnaeus)
- *Ptyas korros (Schlegel)
- Zaocys carinatus (Günther)
- *Lycodon capucinus Boie
- Lycodon laoensis Günther
- Lycodon fasciatus (Anderson)
- Lycodon subcinctus Boie
- *Oligodon cyclurus (Cantor)
- Oligodon purpurascens (Schlegel)
- Oligodon taeniatus (Günther)
- *Oligodon cinereus (Günther)
- *Oligodon quadrilineatus (Jan)
- Oligodon barroni (Smith)
- Oligodon joynsoni (Smith)
- Liopeltis scriptus (Theobald)
- Dryocalamus davidsonii (Blandford)
- Calamaria vermiformis Duméril, Bibron, and Duméril
- Calamaria pavementata Duméril, Bibron, and Duméril
- Plagiopholis nuchalis (Boulenger)
- Pseudorhabdion longiceps (Cantor)
- Ahaetulla formosa Boie
- Ahaetulla caudolineata Gray
- Ahaetulla subocularis (Boulenger)
- Ahaetulla cyanochloris (Wall)
- *Ahaetulla ahaetulla ahaetulla (Linnaeus)

Boiginae

- *Boiga multimaculata (Boie)
- *Boiga cyanea (Duméril, Bibron, and Duméril)
- *Boiga cynodon (Boie)
- Boiga dendrophila dendrophila (Boie)
- *Dryophiops rubescens (Gray)
- *Psammodynastes pulverulentus (Boie)
- Psammophis condanarus indochinensis Smith
- Chrysopelea paradisi Boie
- *Chrysopelea ornata (Shaw)
- *Dryophis prasinus Boie
- Dryophis mycterizans (Linnaeus)
- *Dryophis nasutus (Lacépède)

Natricinae

- *Pseudoxenodon macrops macrops (Blyth)
- Natrix piscator piscator (Schneider)
- *Natrix piscator flavipunctata (Hallowell)
- Natrix trianguligera (Boie)

- Natrix percarinata* (Boulenger)
Natrix inas (Boulenger)
Natrix groundwateri Smith
Natrix deschauenseei Taylor
Natrix modesta (Günther)
Rhabdophis s. subminiata (Schlegel)
**Rhabdophis subminiata helleri* (Schmidt)
**Rhabdophis stolata* (Linnaeus)
**Rhabdophis nigrocincta* (Blyth)
**Rhabdophis chrysarga* (Boie)
Macropisthodon rhodomelas (Boie)
Macropisthodon flaviceps (Duméril and Bibron)
**Parahelicops boonsongi* sp. nov.
Opisthotropis spenceri Smith

Homalopsinae

- **Enhydris plumbea* (Boie)
Enhydris jagorii (Peters)
Enhydris smithi (Boulenger)
**Enhydris enhydris* (Schneider)
Enhydris bocourti (Jan)
[*Enhydris chinensis* (Gray)]
**Homalopsis buccata* (Linnaeus)
Cerberus rhynchops (Schneider)
Bitia hydroides Gray
Herpeton tentaculatum Lacépède

ELAPIDAE

- Bungarus flaviceps* Reinhardt
Bungarus fasciatus (Schneider)
**Bungarus candidus* (Linnaeus)
Callophis maculiceps (Günther)
Callophis gracilis hughii Cochran
Maticora bivirgata (Boie)
Maticora intestinalis (Laurenti)
**Naja naja kaouthia* Lesson in Ferussac
Hamadryas hannah Cantor

HYDROPHIDAE

- Laticauda colubrina* (Schneider)
Laticauda laticaudata (Linnaeus)
Aepyurus eydouxii (Gray)
Kerilia jerdoni siamensis Smith
**Enhydrina schistosa* (Daudin)
**Praescutata viperina* (Schmidt)
Thalassophis anomalus Schmidt
Kolpophis annandalei (Laidlaw)
**Lapemis hardwickii* Gray
Microcephalophis g. gracilis (Shaw)
Pelamis platurus (Linnaeus)
Thalassophina viperina (Schmidt)
**Hydrophis mamillaris* (Daudin)
**Hydrophis caerulescens* (Shaw)

Hydrophis klossi Boulenger
Hydrophis cyanocinctus Daudin
Hydrophis torquatus diadema Günther
Hydrophis torquatus agaardi Smith
Hydrophis ornatus ornatus (Gray)
Hydrophis brookei Günther
Hydrophis fasciatus atriceps Günther

VIPERIDAE

Vipera russellii siamensis Smith

CROTALIDAE

**Agkistrodon rhodostoma* (Boie)
Trimeresurus monticola Günther
Trimeresurus puniceus (Boie)
**Trimeresurus albolabris* Gray
**Trimeresurus popeorum* Smith
Trimeresurus kanburiensis Smith
Trimeresurus purpureomaculatus andersoni Theobald
Trimeresurus wagleri wagleri (Boie)

TAXONOMIC TREATMENT

CLASS AMPHIBIA

FAMILY CAECILIIDAE

Ichthyophis glutinosus (Linnaeus)

Caecilia glutinosa Linnaeus, Systema Naturae, vol. 1, 1758, p. 393 (type locality is here designated by us as Colombo, Ceylon. Linnaeus first described the species in Mus. Adolph Frid., p. 19, tab. 4, fig. 1. The figure probably represents the type).

Two adults, EHT-HMS No. 31729 (RE 4248), 31730 (RE 4263) and seven young, 31731-31737 (RE 4291 young) from Ban Nong Wai (subvillage), Na Phung (village) Dan Sai (district), Loei (province) Thailand on Phu Nam Lang (mt.) elev. approx. 1780 m., Nov. 14-17, 1954, R. E. Elbel coll.

Published data on *Ichthyophis glutinosus* (as well as *I. monochrus*) show a very great range of variation in the number of primary and secondary grooves about the body. We very strongly suspect that more than one form is involved in each species. Boulenger states that the range in number of folds or grooves in *glutinosus* is from 240 to 400, a variation of 160 folds, while in *monochrus* the range is 235 to 360, a variation of 125.

The geographic range is large and an examination of series from various localities will probably demonstrate that the variation mentioned above is geographical. A study of the dentition of individuals of equal age will doubtless prove of much importance in delineating other forms.

The type locality for *I. monochrus* is Sinkawang, Western Borneo. It was collected by Dr. Bleeker and later sent to the British Museum. The type locality for *I. glutinosus* is uncertain. Presumably the origin of the specimen described by Linnaeus is unknown.

One of the earliest descriptions of this species is that of Albertus Seba, Thesaurus, vol. II, 1734, p. 26, pl. 25, fig. 2. The type locality given is Ceylon. The description follows:

Num. 2. Serpens, Caecilia, Ceilonica. Squamis caret: at harum loco tenuibus tegitur annulis, arcte sibi mutuo conjunctis, spadiceo colore tinclis. Alba quasi fascia per ventrem protenditur. Caput peculiare nihil sibi vendicat, praeterquam quod late tumens, binisque amplis naribus, in antica parte, prope os, sit pervium. Linguam in eo reperire non datur, at trachae tamen hiatum. Non

admodum flexilibus est articulis; sed in se ipsam coacta riget. Vide prolegomena.

Since it would appear that no conclusion as to the type locality can now be drawn, we propose to designate Colombo, Ceylon as the type locality. Thus, a study of comparative geographic variation can be made.

The Siamese specimens have the folds numbering 431-438, the primaries and secondaries being of nearly the same length.

The specimens, Nos. 31730 and 31729 yield the following data respectively: Grooves, 431, 438; complete grooves, 64, 66; maxillary teeth, 18-20, 19-?; vomerine teeth, 17-20, 15-?; outer mandibular teeth, 19-20, 19-?; splenial teeth (inner mandibular), 14-14, 15-13; premaxillaries, 5, 5.

It will be noted that the groove-counts of these specimens are considerably higher than the "400" mentioned by Boulenger.

ORDER SALIENTIA

FAMILY RANIDAE

Ooeidozyga lima Kuhl and van Hasselt

Ooeidozyga lima Kuhl and van Hasselt, Isis, 1822, p. 475 (type locality, Java). *Oxyglossis* * *lima* Smith, Journ. Nat. Hist. Soc. Siam, vol. 2, no. 2, Dec. 1916, p. 164 (Klong Wang Hip, Nakon, Sritamarat); *ibid.*, pp. 172-175, pl. (tadpole); Flower, Proc. Zool. Soc. London, Nov. 14, 1899, p. 886. *Ooeidozyga lima* Smith, Proc. Zool. Soc. London, 1927, pp. 202-203; Bull. Raffles Mus., no. 5, 1931, pp. 3-32.

This diminutive aquatic frog is rarely seen out of water. Its habit of resting near the top of the water with only the eyes and nostrils exposed, allows it to become aware of the approach of danger and disappear below the surface with dispatch.

The nostrils are dorsal, nearer the eye than the tip of the snout and surrounded by a slight ridge which develops a papilla on its outer edge. The tympanum, relatively very large, is completely covered by skin so that its outline is not visible without dissection. The inner edge of mandible has a slight shelf which unites anteriorly with one from the opposite side, forming a "second palate" anteriorly which, seen directly from below, entirely or partially conceals the choanae. No vomerine teeth are present. The tongue is pointed posteriorly and free for much of its length.

Externally the body is covered with rough tubercles which on the sides and ventral surface tend to form rows, some bearing a

* Long known under the genus *Oxyglossus* Tschudi (1838) (*non* Swainson); this was replaced by *Oxydozyga* Tschudi (1838) by Stejneger, Proc. U. S. N. M., vol. 66, 1925, p. 33. Later, Malcolm Smith (1927) replaced the latter by the older *Ooeidozyga* Kuhl and van Hasselt, 1822.

series of pores perhaps derived from the neuromast system of the tadpole.

The fingers are pointed, lacking all but a remnant of web, the second longer than the first. The toes are almost completely webbed, the tips of the digits slightly less pointed than the fingers. A prominent tubercle that occurs below the tibiotarsal articulation, that is itself covered with tiny tubercles, will identify the species. The broad median dorsal cream stripe is usually present, as well as the elongate brown stripes on the back of the thighs.

The younger specimens have the upper eyelids heavily tuberculate. The venter is slightly dark with longitudinal rows of silvery-white spots marking the site of low tubercles. As they grow older the dark pigment forms indefinite lines on the chin and on the underside of the thighs, while the dorsum becomes variously lineated. There are however usually two lateral stripes and a pair of dorsal stripes. The latter may be broken leaving short lines and spots. The tuberculation is intensified and practically no area lacks the closely set spiny or rounded tubercles.

The largest specimen, 31720, measures 31 mm. snout to vent. EHT-HMS Nos. 31720-23 (RE 3954) are from Ban Na Phua (sub-village), Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, approx. 200 m. elev., July 28, 1954, Robert E. Elbel and Dr. Boonsong Lekagul, colls. Three specimens, EHT-HMS Nos. 31751-53, That Phanon (city), That Phanon (district) Nakhon Phanom (province), Nov. 20, 1954, Robert E. Elbel, coll.

Phrynoglossus laevis martensii (Peters)

Phrynoglossus martensii Peters, Monatsb. Akad. Wiss. Berlin, 1867, p. 29 (type locality, Bangkok, Siam).

Oxyglossus laevis martensi Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, no. 2, pp. 172-175, pl.; *idem*, vol. 2, no. 2, p. 227 (commonly and widely distributed); *idem*, *ibid.*, pp. 885-916, pls. 59-60.

Phrynoglossus laevis martensi Smith, Bull. Raffles Museum, no. 5, 1931, pp. 3-32.

A very young example of *P. l. martensii* (KUMNH No. 40195) is from Pakchong (village), Sikiu (district), Khorat (province), Thailand, taken Aug. 23, 1952 and a second, older specimen (EHT-HMS No. 31837) is from Udon Thani (city), Udon Thani (province), Thailand, both specimens obtained by the junior author.

In No. 31837 the following characters may be discerned. The snout is very flat, bluntly rounded when seen from above, without trace of a canthus rostralis. The nostrils are widely separated, the distance between them slightly greater than the interorbital distance. The nostril is nearer the eye than the median point on the upper lip. The tympanum is large, covered with skin but its outline can

be seen, its diameter a little more than half of the length of the eye. A fold of skin from the eye runs over and behind the tympanum and on to the side of the neck.

The tongue is elongate oval, rounded behind, free on the sides, not or but slightly free behind. The vocal sac is present, the two slits being at the level of the back of the tongue. The two palatal shelves meet anteriorly forming a platform which does not conceal the choanae when seen from below. Eustachian tube openings larger than choanae. There are no vomerine teeth, but lying back of choanae, and between their inner levels, there are two heavily pigmented areas. The first finger is longer and larger than the second, the inner digits with a lateral fringe or ridge extending to the tips, no web or only a remnant of a web. The toes are three-fourths to four-fifths webbed, the tips feebly dilated. An enlarged compressed inner metatarsal tubercle about three-fifths as long as the first toe. There is no tarsal fold or tubercle. The metatarsals are united.

The skin on the head and dorsum is smooth but on the sides there is a series of five or more pustules, some other indefinite granules, and often small granules about the vent. The chin is smooth but the venter is traversed by numerous fine well-marked wrinkles. The thigh is smooth on the underside.

The color is brown lavender with a median cream stripe. Four very indefinite darker stripes can be discerned when the specimen is submerged in a clear liquid. The tibia and tarsus have one or more indistinct darker bands. The chin and throat are brown, heavily stippled with cream.

Measurements in mm.: Snout to vent, 21; width of head, 8; length of head, 7.7; arm, 11.2; leg, 31.7.

We follow Malcolm Smith in regarding the genus *Phrynoglossus* valid, and not a synonym of *Ooeidozyga*.

Rana tigerina * *pantherina* (Fitzinger)

Hydrostentor pantherinus Fitzinger, *Ausb. österr. Naturf., Sitz. kais. Akad.* Band 42, p. 414 (type locality, Hong Kong).

Rana tigrina pantherina Steindachner, *Reise der Österreichischen Fregatte, Novara, um die Erde im 1857, 1858, 1859. Amphibien, Zool. Theil, Bd. 1*, 1867, p. 17, pl. 1, figs. 14-17; Boulenger, *Rec. Ind. Mus.*, vol. 20, June 1920, p. 17.

Three specimens of *Rana tigerina pantherina* are in the collection. These are: EHT-HMS Nos. 31820 (RE 3674), Phu Phan (mt.),

* Daudin spells the specific name of this species *tigerina* (*Histoire naturelle des rainettes des grenouilles des crapauds. An. XI (1803), p. 64, pl. 20*). This can scarcely be regarded as a typographical error since it is so spelled by Daudin in *Histoire naturelle générale et particulière des reptiles, tome 8, An. XI (1803), p. 125-126*.

550 m., Sakon Nakhon (district), Sakon Nakhon (province), June 12, 1954, Dr. Boonsong Lekagul and Robert E. Elbel colls.; No. 31692 (RE 4018), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), approx. 1780 m. "same range as Phu Nam Lang (mt.) but north." September 29, 1954, Robert E. Elbel coll.; and No. 31821 (RE 4255), Ban Nong Wai (subvillage), Na Phung (village), Dan Sai (district), Loei (province), approx. 1780 m. "range of Phu Nam Lang (mt.)", Nov. 15, 1954, Robert E. Elbel coll.

The largest specimen, 31692, measures 104 mm. from snout to vent. The femora have been broken by the collector so that accurate measurements of the legs cannot be made. The toes are about four-fifths webbed, the tips rounded into tiny discs. There is a free skin-flap on the outer edge of the fifth toe, and a slight ridge or fringe on the inner side of the first toe. The skin-fold above the tympanum curves down closely behind the tympanum. The dorsal folds are discontinuous on each side forming five to seven irregular lines of short glandular ridges, which reach to the groin or onto the rump. There is a pointed median denticulation on the lower jaw with two shorter ones on each side.

On the body there are numerous scattered black or dark brown spots, many associated with glandular ridges. The back part of the thigh is dark brown reticulated with cream, as is the front side of the femur, tibia and the lower part of the sides. The chin and throat are cream with a series of more or less symmetrical lines and spots. The upper lip bears cream spots surrounded by brown. The top of the head is nearly uniform brown and the venter nearly uniform cream.

The other two specimens are marked in much the same manner. The ridges on No. 31820 are somewhat more elongate. The tibiotarsal joint reaches the nostril. In No. 31821 the joint reaches the eye. In all, the first finger is longer than the second. Its tip may be somewhat better developed into a rounded disc than those on the other fingers. The inner side of the second and third fingers have a distinct lateral fringe.

Rana limnocharis limnocharis Gravenhorst

(Fig. 2)

Rana limnocharis Gravenhorst, Deliciae Musei Zoologici Vratislaviensis continens Chelonias et Batrachia, Fasc. 1, Lipsiae, 1829, p. 42 (type locality, Java).

Specimens of *Rana limnocharis* in the collection are from the following localities: EHT-HMS No. 31778 (RE 3674), Phu Phan

(mt.), 550 m., Sakon Nakhon (district), Sakon Nakhon (province), June 12, 1954, "large gravid female 59 mm. snout to vent"; Dr. B. Lekagul and R. E. Elbel colls. No. 31750 (RE 3954) (lot of two, one very young) from Ban Na Phua (subvillage), Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand,



FIG. 2. *Rana l. limnocharis* Gravenhorst, EHT-HMS No. 31778 ♀ Phu Phan (mt.), Sakon Nakhon (district and province), Thailand. Actual snout-vent length, 41.

"on the edge of the range of Phu Phan (mt.), 200 m. elevation"; Sept. 29, 1954. Nos. 31776-77 (RE 4018), from Ban Na Muang (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand; Sept. 29, 1954, R. E. Elbel coll. KUMNH Nos. 40186, 40188 (both RE 3259), Phu Kading (mt.), 1045 m., Si Than (village), Wang Saphung (district), Loei (province), Thailand,

Jan. 4, 1954; Dr. B. Lekagul and R. E. Elbel colls. Nos. 40008-40009, Thailand, Feb. 1955 (no locality data); 40012, Phathalung, Thailand, Feb. 1955; 40013, Mae Hong Son, Thailand, Feb. 1955, Dr. Boonsong Lekagul coll.

One peculiar character* evident in these specimens is the presence of a ventral area outlined by a slight groove or fold that crosses the breast, passes to a point on side behind the axilla, then runs back to the median point between thighs. This line represents the line of attachment between the skin and the muscles below. In males at least the entire area is glandular and at certain times produces a covering of minute granulations most conspicuous on the area following the breast. There is also a slight fold running from the breast to the angle of the mouth. These are always evident but are very conspicuous in the gravid female.

The male usually may be distinguished by its smaller size and the deep black coloring of the vocal-sac area on the chin and throat. A median cream line may be present or absent in either sex. This species is common everywhere in Thailand except in high mountains.

Rana macrodon Kuhl

Rana macrodon † Kuhl, in Tschudi, Classification der Batrachier, 1838, and in Mém. Soc. Sci. Nat. Neuchâtel, vol. 2, 1839, p. 80 (attributes the name to Kuhl), (type locality, Java).

Rana macrodon var *blythi** Boulenger, Rec. Ind. Mus., vol. 20, pp. 40-45, part. Nakon Sritamarat (=Nakon Si Thammarat) type locality.

The following specimens are in the collection: KUMNH No. 40014 ♀ Nakhon Si Thammarat, "Thailand"; 40015 yg. "Thailand"; 40016 "Thailand" collected by Dr. Boonsong Lekagul.

The first two specimens have been eviscerated. The third (No. 40016) is a male approximately 120 mm. snout-vent length; head width, 46 mm.; length of head, 52 mm. In this specimen the diameter of the tympanum (8 mm.) is less than the length of eye (11 mm.). The elongate toothlike projections from the anterior part of the lower jaws reach an elevation of almost four millimeters. The vomerine teeth are in two compressed elevated ridges, diagonally placed, reaching from a point a little distance in front of choanal level to a point considerably behind posterior choanal level; palatal glands open in an irregular curved series of thirteen pores nearly midway between the anterior choanal level and the anterior

* This character is present in certain other species of *Rana* but is never conspicuous.

† Malcolm Smith (1930) regards *blythi* as a form not easily differentiated from *macrodon*, and Boulenger later states that the name in "a racial sense cannot be used." The association of *Rana magna* and *Rana acanthi* with *macrodon* as subspecies, as recently proposed, we believe should be disregarded.

part of palate; the jaw denticulations fit into deep depressions in the upper jaw.

In No. 40014 ♀ the tympanum is a little less than 5 mm. in diameter and its shape is oval rather than round. The snout-to-vent length is 102 mm.

Rana macrognatha macrognatha Boulenger

(Fig. 3)

Rana macrognatha Boulenger, Ann. Mag. Nat. Hist., ser. 8, vol. 20, p. 414; Rec. Ind. Mus., vol. 20, p. 51 (type locality, Karin Hills, Burma).

Rana macrognatha macrognatha M. Smith, Jour. Nat. Hist., Soc. Siam, vol. IV, no. 4, July 25, 1923, pp. 218-219, pl. 9, fig. 2 (adult male head; Nakon Sritamarat Mts., Siam).

Two specimens, EHT-HMS Nos. 31724 ♀, 31725 ♂ (Lot RE 3820), were taken at Phu Phan (mt.), Sakon Nakhon (district), Sakon Nakhon (province), Thailand, at an elevation of 550 m., June 29, 1954, by Dr. Boonsong Lekagul and Robert E. Elbel.

Diagnosis: Head of male broad (25.5 mm.) equally as broad as long, more than half the length of head and body; leg short, the tibiotarsal articulation reaching to anterior part of eye; first finger slightly longer than second; a free-edged flap or swelling beginning between orbits extends some distance behind them; a slight swelling on sides of occiput behind eyes; no dorsolateral glandular fold. Diameter of tympanum equals length of eye in male; no glands below tympanum or on humerus; skin covered with minute granules intermixed with larger, often pearly-tipped pustules.

Description of No. 31725 ♂: A median pointed denticulation on lower jaw flanked on each side by a broad-based, sharply pointed spine, which fits into a slight depression of the upper jaw; choanae partly concealed by shelf on maxillary when seen from below; vomerine teeth (three to five in number) on two converging diagonal ridges, largely behind posterior level of choanae, separated widely from choanae and from each other; openings to vocal sac are behind tongue, the openings small, puckered; posterior horns of tongue prominent, the tongue narrowly free behind (in female more than a third free). Palatal glands open through two canals each with a small opening that is closer to level of choanae than to front end of palate.

Distance between nostrils equal to their distance from eye and from the median point on upper lip; canthus rostralis not evident; width of an upper eyelid less than interorbital width; between orbits a tongue-like raised area extending from front of eyes back onto occiput, the posterior edge free, rounded; occipital area swollen



FIG. 3. *Rana macrognatha macrognatha* Boulenger. Upper figure EHT-HMS No. 31724 ♀. Actual snout-vent length 49 mm.; lower EHT-HMS No. 31725 ♂. Actual snout-vent length, 50 mm. Both from Phu Phan (mt.), Sakon Nakhon (district and province), Thailand.

on each side posterior to eye; tympanum distinct, its diameter equals eye length, covered with closely adherent skin, the surface with minute granules; no glands present at mouth angle or below tympanum and none on humerus; an inverted V-shaped fold back of occiput; two more or less distinct rows of elongated pustules behind tympanum extending to groin; dorsum and limbs with smaller pustules, those on limbs usually arranged in indefinite longitudinal rows, the pustules with pearly tips; chin with a few indistinct longitudinal wrinkles; venter with very numerous, moderately distinct transverse folds or wrinkles; a fold across breast reaches to near mouth angle; median and posterior ventral part of thigh with large granules. Arms short, the first finger slightly longer than the second; a narrow fringe along part of inner side of the second and third fingers; subarticular tubercles well developed; three palmar (metacarpal) tubercles, innermost elevated, outermost elongated.

Legs short, when folded at right angles the heels barely touch; the tibiotarsal articulation reaches front edge of eye. An elongate inner metatarsal tubercle in line with a distinct tarsal fold and a fold or fringe that extends along outer edge of inner toe; no outer metatarsal tubercle; a fringe along outer edge of fifth toe; outer metatarsals separated by a web; distinct discs on toes, with a groove on outer edge; toes about three-fourths webbed.

Color: In preservative the frontal and interorbital areas light brown; occiput darker brown, the color running forward on each side onto eyelids; sides a little darker than the light brown back; legs barred with dark brown; soles of feet brown. Venter and underside of limbs cream; brown spots on upper and lower jaws; tympanic area light tan.

Measurements in mm.: (♂ and ♀): Snout to vent, 50, 49; head length, 26, 21; axilla to groin, 19, 20; arm, 26, 27; leg, 67, 72; tibia, 24, 22; foot, 31.5, 31.

Remarks: The specimen from the same locality, identified as the female of the species, lacks the specialization of the head of the male. There is a strongly defined cream stripe on the head and body from lip to near vent; the fold across the breast and shoulders is more distinct. Toothlike projections on the jaws are only slightly indicated; and the upper eyelid is as wide as the interorbital distance. The diameter of the tympanum is about three-fourths of the length of the eye. Variation in the width of the head is indicated in the measurements.

Rana kuhli Schlegel

(Fig. 4)

Rana kuhli (Schlegel [Mus. Ludwig Batavia]) Duméril and Bibron, *Erpétologie Générale*. . . ., vol. 8, 1841, pp. 384-386 (type locality, Java); Smith, *Jour. Nat. Hist. Soc. Siam*, vol. 2, May 1917, p. 227 (peninsular, western, and northern Siam: common on many of the hills above 300 m.); *idem*, vol. 2, no. 4, Dec. 1917, pp. 262-263, pl. fig. 1 (tadpole), (Doi Nga Chang, March, 700-1000 m. elev.); Günther, *Reptiles of British India*, 1864, pp. 404-405, pl. XXVI, fig. A (but not fig. B) (*part*).

The following specimens are in the collection: KUMNH No. 40185 (RE 3156), Khao Sawan (mt.), approx. 600 m. elev., Sieo (village), Loei (district and province), Thailand, Nov. 23, 1953, Dr. Boonsong Lekagul and Robert E. Elbel, collectors. Nos. 40189-40190 (RE 3236), Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, Dec. 10, 1953 (approx. 600 m. elev.) Dr. Boonsong Lekagul and Robert E. Elbel,



FIG. 4. *Rana kuhli* Schlegel. EHT-HMS No. 31738 Ban Na Muang, Na Haeo (village), Dan Sai (district), Loei (province), Thailand. Actual snout-vent length, 72 mm.

collectors. EHT-HMS Nos. 31738-31739 (RE 4018), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand (approx. 1780 m. elev. and in the same range as Phu Nam Lang (mt.) but farther north), Sept. 29, 1954, Robert E. Elbel, collector.

This common form is characterized by a wide, rather depressed head crossed by a white or cream bar. Taylor (1934) has inadvertently recorded this frog from "Chiang Mai," Thailand, as *Rana corrugata*.

Rana cubitalis Smith

(Fig. 5)

Rana cubitalis M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, 1917, p. 277 (type locality, Doi Nga Chang, Thailand); Rec. Ind. Mus., vol. 26, 1925, p. 138 (tadpole); Boulenger, Rec. Ind. Mus., vol. 20, June, 1920, p. 138, 139 (redescription of ♂ type from "Doi Nga Chang, Thailand, 1600 ft. elev."); M. Smith, Bull. Raffles Museum, no. 3, Apr. 1930, pp. 103-104, fig. 5 ([arm, showing gland] mountains of Nakon Sritamarat, Thailand; Karen Hills, Burma).

Three specimens of this handsome frog (EHT-HMS Nos. 31747-49 [RE 3986]) are in the collections. They are from Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, approx. 1780 m. elevation. Sept. 25, 1954, Robert E. Elbel, collector. One is a male, two are females.

The male seems to differ from the females not only in the presence in the glandular development of the first finger and the large gland on the forearm, but also in having the fine granulations of the back interspersed with numerous granules and larger pustules. The sides are covered with very numerous pustules each in turn covered with numerous fine spinous granules (ten to forty). The granules and pustules on the femora tend to form longitudinal rows while on the tibia they tend to unite into elongate glandular folds. There is no distinct tarsal fold but a slight rounding elevated ridge follows the inner edge of the tarsus and there is a very slight outer line of minute granules continued onto the edge of the fifth toe; two strong metatarsal tubercles are present. Four or five vomerine teeth are present on ridges lying between the choanae. The ridges are separated from each other by a distance equal to the length of one ridge, and from the choanae by an equal distance. The vocal openings are small and situated in the floor of the mouth behind level of tongue.

The color of the male is very light brownish-gray with a brown blotch indicated in the tympanic area and a brown stripe present

below the canthus rostralis. The anterior part of the narrow dorso-lateral glandular ridge has a blackish brown border. The limbs have only a suggestion of transverse markings. The venter is



FIG. 5. *Rana cubitalis* M. Smith. EHT-HMS No. 31748♀ Ban Na Muang, Na Haeo (village), Dan Sai (district), Loei (province), Thailand. Actual snout-vent length, 76 mm.

smooth or with only fine transverse wrinkles. On the posterior face of the thighs there are granules or areolae.

The females, much larger and gravid, have the dorsum fawn to buff-brown with a brown line strongly defined in the loreal region and on the tympanum. A brown line is present on the under-

side of the arm near its insertion. A few flecks of brown are on the lower jaw and a few scattered brown spots are present on the sides and along the dorsolateral glandular fold. They are pronounced on the anterior face of the thigh, tibia and tarsus. The foot and underside of tarsus are dark lavender-brown. The venter and the underside of the thighs are uniform light (cream?). The chin and throat have scattered dark pigment in one female, while in the other the entire ventral surfaces of the body and limbs are immaculate.

We do not find the openings of the palatal glands on the palate in front of the vomerine teeth in either sex.

Annandale (Mem. Asiat. Soc. Bengal, vol. 6, 1917, pp. 141-142, fig. 5 [head]) gives a brief description of frog specimens from Pegu, lower Burma, under the name of *Rana leptoglossa* Cope. From the figure given we would guess that it is actually a member of this species which was described in 1917.

Rana nigrovittata (Blyth)

(Figs. 6 and 7)

Lymnodytes nigrovittata Blyth, Jour. Asiat. Soc. Bengal, vol. 24, 1855, p. 718 (type locality, Mergui, Tenasserim).

The following specimens, collected by Robert E. Elbel and Boonsong Lekagul, are referred to *Rana nigrovittata*: KUMNH Nos. 40182-40184 (RE 3420), Ban Sang Kho, (subvillage), Khok Phu (village), Sakon Nakhon (district and province), Thailand, Feb. 9, 1954, elev. approx. 500 m.; No. 40188 (RE 3259), Phu Kading (mt.), elev. 1045 m., Si Than (village), Wang Saphung (district), Loei (province), Thailand, Jan. 4, 1954, EHT-HMS No. 31772 (RE 3820), Phu Phan (mt.), elev. 500 m., Sakon Nakhon (district), Sakon Nakhon (province), Thailand, June 29, 1954.

This last specimen, a male, differs from the descriptions of this species in having large moundlike areas, resembling paratoids, between the tympani, narrowly separated from the orbits, and caused seemingly by hypertrophy of muscles below the skin. We give it herewith a detailed description. However, it seems to agree reasonably well with *R. nigrovittata* Blyth.

Diagnosis: A pair of well-defined dorsolateral folds; interorbital space wider than upper eyelid; an internal vocal sac, the openings small, puckered, very far back in mouth; a well-defined gland on humerus near the insertion of the arm; skin minutely and uniformly granular except on posterior part of rump, where part of



FIG. 6. *Rana nigrovittata* (Blyth). KUMNH No. 40188, Phu Kading (mt.), 1045 m. elev., Si Than, Wang Saphung (district), Loei (province), Thailand. Actual snout-vent length, 57 mm.

the granules are larger; toes three-fourths to four-fifths webbed, the toes with moderately large discs.

Description of species: Head obtusely pointed the width of the head distinctly greater than its length; canthus rostralis indicated, rounded; loreal region concave; nostril about equidistant between eye and the median point on upper lip; interorbital area wider than the upper eyelid; tympanum large, distinct, superficial, not covered by skin, its greatest diameter (6.2 mm.) much less than

length of eye (9.1 mm.), separated from the eye by a distance of four millimeters; no distinct gland below tympanum (however, the skin on upper jaw is thickened somewhat and now softened).



FIG. 7. *Rana nigrovittata* (Blyth). EHT-HMS No. 31772, Phu Phan (mt.), 500 m. elev., Sakon Nakhon (district and province), Thailand. Actual snout-vent length, 70 mm.

Tongue elongate, notched, with two rounded processes behind, free for about one fourth of its length; choanae lateral; two bony ridges at anterior level of the choanae extending back of their posterior level, separated from choanae by a distance equal to their distance from each other, bearing two vomerine teeth on the posterior end of each ridge. A median denticulation on lower

jaws; no lateral denticulations but a thickening of the anterior part of the jaw is evident. First finger longer than second; subarticular tubercles large. Three large metacarpal tubercles, the two outer partially fused posteriorly; four supernumerary tubercles; leg elongate, the tibiotarsal articulation reaches the tip of the snout; no dorsal fold; two metatarsal tubercles the inner twice as long as wide, the outer distinct, rounded; no fringe on outer side of fifth and inner side of first digits; disks well-developed, edged by a groove; outer metatarsals separated by a web; toes from three-fourths (on inner) to four-fifths webbed on outer fingers; subarticular tubercles large.

Skin above on head and body with very small uniform granules but becoming a little larger on rump; a few larger tubercles on back part of upper eyelid; no distinguishable fold behind tympanum; sides indistinctly granular, the granules of variable size; chin and venter smooth; area on posterior face of thighs granular; most of ventral surface of thighs glassy smooth; upper surface of tibia and tarsus with fine spiny tubercles, often pearl-tipped. A pair of dorsolateral glandular folds.

Color, in preservative: Above uniform brown, the swollen areas on occiput distinctly lighter; sides of snout dark brown; a lateral brown stripe, lighter back of eye, darkest along outer edge of the dorsolateral fold; arms dark brown above with some brown spots with lighter background on posterior ventral surface; leg with irregular dark bars above composed of coalescing spots; back surface of femur brown reticulated with light brown; chin and throat, venter and underside of limbs with fine brown pigment; the spotting on the legs extends onto the undersides; palms light, soles blackish brown; upper jaw with a brownish-gray stripe extending to below tympanum.

Measurements in mm.: No. 31772: snout to vent, 70; width of head, 31; length of head, 27; arm, 42; leg from vent, 113; tibia, 38; foot, 51.

Remarks: The three additional specimens listed are females and lack the humeral gland. Below the tympanum are two distinct glandular areas. In these specimens, a groove, midway between the anterior level of the choanae and front of the palate, marks the outlets of the palatal glands. We cannot find this in the male specimen, and it may represent another significant difference in populations.

Rana erythraea (Schlegel)

(Fig. 8)

Hyla erythraea Schlegel, Abbildungen neuer oder unvollständig bekannter Amphibien . . ., 1837, p. 27, pl. 9, fig. 3.

Eleven *Rana erythraea* (EHT-HMS Nos. 31681-31691 [Lot RE 4292] were collected at Ban Nong Wai (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Nov. 17, 1954, by R. E. Elbel. All are of medium size, 35 to 42 mm. in snout-vent length. The green dorsal color has disappeared but the dorsolateral cream stripes covering the broad dorsolateral glandular fold are strongly in evidence.

The species attains a length of 78 mm. for females; 42 for males. It is widespread in the lowlands in southeastern Asia and Indonesia. The senior author has reported it on certain of the Philippine Islands.

Rana chalconota (Schlegel)

Hyla chalconota Schlegel, Abbildungen neuer oder unvollständig bekannter Amphibien . . ., 1837, p. 24, pl. 9,* fig. 1.

A single poorly preserved specimen of *Rana chalconota* from Ban Chawang (village), Chawang Sieo (district), Nakhon Si Thammarat (province), Thailand is in the collection. It bears the KUMNH number 40007 (BL 20094). It was taken Feb. 1954 by Dr. Boonsong Lekagul.

Rana sp.

Nine tadpoles of an unidentified Anuran, presumed to be a *Rana* were taken on Khao Sawan (mt.), approx. 600 m. elev., Sieo (village), Loei (district and province), Thailand, by Dr. Boonsong Lekagul and R. E. Elbel, Nov. 29, 1953. The lot is numbered EHT-HMS No. 31841 (RE 3173). While these have been somewhat discolored by preservatives a median lighter muscular area beginning in the occipital region is evident. Near the beginning of the tail are two somewhat diagonal, rather large discrete brown spots closely approximated. A transverse bar or spot is present somewhat in advance of these and a median dark spot is present in the occipital area. The frontal region may have a few darker flecks or spots. A few small brown spots occur on the caudal fin and tail. The spiracle is sinistral; the anus dextral.

The mouth is surrounded by a papillate fringe. At the anterior median point is a short curved tooth series. The upper beak is of blackish horn as is the lower. Both are denticulate. On each side

* Van Kampen (1923) regards fig. 3 of pl. 50, the illustration of this species (not fig. 1, pl. 9).



FIG. 8. *Rana erythraea* (Schlegel). Upper EHT-HMS No. 31684. Actual snout-vent length, 41 mm.; lower EHT-HMS No. 31689, actual snout-vent length, 40 mm. Both from Ban Nong Wai, Na Phung, Dan Sai, Loei (province), Thailand.

of the upper beak are five series of denticulations, diminishing in length posteriorly. The beak on the lower jaw is narrower than upper. On each side and extending somewhat posterior to it are five rows of denticulations growing longer toward the lower edge of the frill; on each side are about 25 very short fragmentary rows of denticulations. At most posterior part of area a median flat pad-like region edged anteriorly with denticulations.

Micrixalus magnapustulosus sp. nov.

(Fig. 9)

Type: EHT-HMS No. 31838 ♂, Ban Na Phua (subvillage), Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, elevation approx. 200 m., collected July 28, 1954, by R. E. Elbel and Dr. B. Lekagul.

Diagnosis: A diminutive frog with unnotched tongue a little longer than wide, free laterally and free posteriorly for about one



FIG. 9. *Micrixalus magnapustulosus* sp. nov. Type EHT-HMS No. 31838 ♂, Ban Na Phua, Kan Luang, Na Kae (district), Nakhon Phanom (province), Thailand. Actual snout-vent length, 16 mm.

third of its length; no trace of vomerine teeth; lower jaw symphysis with a suggestion of a median denticulation; eye large, longer than snout (measured mesially); a sinuous fold from corner of eye behind and partly across tympanum to above arm insertion; tympanum covered with skin but its outline partly discernible; a curving fold runs from corner of mouth; dorsum and sides with numerous large pearl-tipped pustules, the skin between them with smaller pustules or roughened ridges; toes four-fifths webbed, the web reaching at least the small, slightly rounded tip of the fourth toe.

Description of the type: Tip of the snout broadly oval, the nostrils slightly elevated, situated about an equal distance from the eye and the median point on edge of upper lip, separated from each other by a distance equal to or very slightly less than median length of snout; width of an eyelid equal to or slightly less than the inter-orbital distance; tympanum covered with skin but moderately distinct, its diameter (1.5 mm.) much less than length of eye-opening (2.2 mm.); a sinuous fold from eye runs downward and backward behind tympanum and terminates on shoulder above the insertion of arm; a small curving fold runs back for a short distance behind mouth-angle; no canthus rostralis; the loreal area slightly convex rather than excavated; snout extends beyond mouth for about half a millimeter; eye large, strongly elevated, its length greater than median length of snout, but equal to a line from eye to the middle point on upper lip.

Tongue a little longer than wide (3×2.7 mm.), free posteriorly for more than a fourth of its length, and free laterally; no tongue papilla, but the surface minutely granular; choanae small, nearly lateral, not concealed by maxillary shelf when seen from below; no trace of vomerine teeth; openings of the Eustachian tubes smaller than choanae; no evidence of vocal slits. The symphysis of the lower jaws has no denticulate elevation.

Arm short, only the toes reaching beyond tip of snout; first finger very little longer than second; only a mere vestige of a web, the edges of the digits not or but slightly ridged on sides. Three small palmar tubercles the inner and outer a little more distinct than middle one, the outer elongated and completely separated from the middle one; four distinct subarticular tubercles.

Leg short, the tibiotarsal articulation reaches the middle of the eye; toes with only a slight development of the terminal discs, the web reaching the discs on one or more toes; a well-defined, somewhat compressed, elongate inner metatarsal tubercle; a very tiny

outer tubercle situated at the terminus of a slight pustular ridge along outer toe; well-developed subarticular tubercles; a short diagonal tarsal fold extending less than half length of tarsus; when legs are folded at right angles to body the heels fail to touch.

Skin on snout and interorbital area with a very indistinct elevation across head between anterior edges of eyes (the "eyespot" included); body with large craterlike pustules, the sides of which are excavated by numerous "valleys"; pustules pearl-tipped, between larger pustules are tiny pustules or ridges; sides with less distinct pustules; legs with numerous smaller pearl-tipped pustules tending to form longitudinal rows; chin nearly smooth; venter without distinct granules; underside of thighs smooth except on the posterior part; posterior face of thighs have a very few scattered granules.

Color in preservative: Generally brown above with two vague lighter areas on middle of back preceded and followed by slightly darker areas or lines; upper side of upper arm fawn brown, the forearm banded with brown. Leg, including tarsus, and foot, with narrow bands; chin and throat brownish with some lighter flecks; venter and part of underside of thighs nearly immaculate; soles dark lavender.

Measurements in mm.: Snout to vent, 16; width of head, 7; length of head, 6; arm, 8; leg, 22.5; tibia, 7; foot, 7.7.

Remarks. We are unable to determine the age of the specimen but believe it to be nearly adult, nor can we state certainly the character of the pupil, but believe it to be horizontal.

FAMILY RHACOPHORIDAE

Rhacophorus leucomystax leucomystax (Gravenhorst)

(Fig. 10)

Hyla leucomystax Gravenhorst, *Deliciae Musei Zoologici Vratislaviensis continens Chelonias et Batrachia*, fasc. 1, Lipsiae, 1829, p. 26.

Rhacophorus leucomystax Smith, *Jour. Nat. Hist. Soc. Siam*, vol. 2, no. 3, p. 229. Flower, *Proc. Zool. Soc. London*, Nov. 14, 1899, pp. 898-899, pl. 59, figs. 3, 3a (tadpoles).

Polypedates leucomystax leucomystax Taylor, *Proc. Acad. Nat. Sci. Philadelphia*, vol. 86, 1934, p. 283 (Chieng Mai).

Two specimens of this arboreal species (KUMNH Nos. 40193-94 [RE 3034]) are from Khon Kaen (city and province), Thailand, Nov. 13-14, 1953, Robert E. Elbel, coll., and one, No. 40017 is from Thailand without definite locality. Two of them (40193-94) are marked on dorsum with dark gray or brownish spots on a gray background; the third, No. 40017, is nearly uniform gray with some very indefinite mottling. The limbs of all specimens are barred dimly

with darker color. On the sides there may be a row of dark spots, as if a dark stripe beginning behind eye and passing through tympanum and beyond had been broken up. A very narrow cream line borders the lip in all of the specimens.

The posterior face of the thigh is brown, this color enclosing cream spots or flecks, while a similar coloration is dimly indicated



FIG. 10. *Rhacophorus leucomystax leucomystax* (Gravenhorst). KUMNH No. 40194 Khon Kaen (city and province), Thailand. Actual snout-vent length, 60 mm.

on the front of the thigh and groin areas. A small postcranial fold is indicated.

The palatal glands open in a transverse line of eight pores about midway between the anterior point of the palate and the anterior level of the choanae. The vomerine teeth are 8-10 on two converging ridges beginning on the anterior level of the choanae and terminating near their posterior level. The subtriangular openings

of the Eustachian tubes are of smaller area than the choanal openings.

The webbing on the hand is reduced to a vestige between the first three fingers; no web is evident between the two outer fingers. The webbing of the toes becomes progressively greater. The two inner toes are less than half webbed, while the other toes are from one-half to three-fourths webbed.

The pads have a deep groove around their outer edges and each is traversed by a groove somewhat posterior to the center on the underside.

No. 40017 has a more extensive web, the web reaching the base of the pads on some of the toes.

FAMILY MICROHYLIDAE

Microhyla berdmorei (Blyth)

(Fig. 11)

Engystoma (?) *berdmorei* Blyth, Jour. Asiat. Soc. Bengal, vol. 24, 1856, p. 720 (type locality, Pegu, Burma).

Microhyla berdmorei Parker, A monograph of the frogs of the family Microhylidae. 1934, pp. 127-28 (synonymy and distribution).

Microhyla fowleri Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, pp. 284-86, fig. 1, pl. 17, fig. 2 (type locality, Chieng Mai, Siam).

Microhyla malcolmi Cochran, Proc. Biol. Soc. Washington, vol. 40, 1927, p. 182 (type locality, Pak Jong, Siam).

A specimen of *Microhyla berdmorei* (KUMNH No. 40019) is in the collection from Phatthalung, Thailand, Dr. Boonsong Lekagul, coll. It is a female with the abdomen distended with eggs.

The following structural characters obtain in this specimen:

Diagnosis: A median groove present on the upper surface of the widened digital discs producing two separate elevations. Snout longer than eye; a rounded canthus rostralis; three palmar tubercles, the two outer closely approximated; two small rounded metatarsal tubercles; tibiotarsal joint extends about six millimeters beyond the tip of snout; venter and underside of limbs glassy smooth.

Description of species: Tip of snout forming a narrow oval, projecting beyond mouth 1.8 mm.; nostril equidistant between eye and the median point on upper lip; loreal region not concave; tympanum concealed by skin and partly covered by muscles; tongue narrowed anteriorly, widened posteriorly, free for half its length; shelf on the inner side of the maxillary joins with its fellow firmly to form a small anterior platform that does not conceal the choanae when seen from below; latter small, transversely oval; a rather broad transverse ridge across palate in front of oesophageal opening.

Skin smooth above and below (perhaps more so than normal because of the distension of the skin caused by the eggs within); the fingers reach beyond tip of snout when arm is laid forward; first finger much shorter than second, which in turn is shorter than the fourth; edges of fingers with slight lateral ridges but web is lacking except for the merest remnant; subarticular tubercles prominent;



FIG. 11. *Microhyla berdmorei* (Blyth). KUMNH No. 40187, Phu Kading (mt.), 1045 m., Si Than, Wang Saphung (district), Loei (province), Thailand. Actual snout-vent length, 39 mm.

palmar tubercles three, the two outer almost united, partially separated by a narrow groove.

Terminal pads scarcely wider than fingers, divided by a groove above, forming two small swellings on dorsal part of pad. Toes completely webbed, the tips of the toes widened and divided above by a groove forming two "scalelike" swellings; outer metatarsals united. Legs long, the tibiotarsal joint extending several milli-

meters beyond tip of snout; heels overlap ten millimeters when legs are folded at right angles.

Color: Purplish above becoming lavender-brown on sides. There is trace of a bar between eyes which begins a darker area that narrows on occiput, widens again on shoulders and then becomes lost on back. Some black rounded spots above and behind arm insertion; black spots on front of thigh and on the posteroventral region on tibia; underside of chin heavily mottled with brown; underside of tarsus and foot purplish brown; ventral surface of body and limbs largely cream. A triangular black mark in anal region.

Measurements in mm.: Snout to vent, 41; width of head at tympanum, 12.3; length of head, 16; arm, 20; leg, 77; tibia, 27; foot, 34.

A second specimen KUMNH No. 40187 (RE 3254), also a gravid female, agrees in most details with the preceding. It is from Phu Kading (mt.), 1045 m. elev., Si Than (village), Wang Saphung (district), Loei (province), Thailand, Jan. 1, 1954, R. E. Elbel and Dr. B. Lekagul, colls.

Kaloula pulchra pulchra Gray

Kaloula pulchra Gray, The zoological miscellany, 1831, p. 38 (type locality, "China"); Taylor, Proc. Acad. Nat. Sci. Philadelphia, vol. 86, 1934, p. 284, pl. 17, fig. 1 (Chieng Mai, Siam).

Callula pulchra Günther, Reptiles of British India, 1864, p. 437 (Siam, etc.); Boulenger, Catalogue of the Batrachia Salientia and Ecaudata in the collection of the British Museum, 2nd ed., 1882, pp. 170-171, figs. (Siam, etc.); Nieden, Das Tierreich, Anura II. Lief. 49, 1926, pp. 22-23, fig. 18; Jour. Nat. Hist. Soc. Siam, vol. 2, no. 1, June, 1916, pp. 40-41; *idem*, vol. 2, No. 3, May, 1917, 226-231 (common and widely distributed in Siam).

Kaloula pulchra pulchra Parker, A monograph of the frogs of the family Microhylidae, London, 1934, pp. 84-86 (Bangkok, Chantaboon; literature list and synonymy).

A large specimen of *Kaloula p. pulchra* (KUMNH No. 31516) from Rat Buri, Thailand was collected by Dr. Boonsong Lekagul. The typical coloration is present. It measures 67 mm. in length.

The choanae, due to the extremely short snout, are at the anterior end of the palate. They are transversely widened and followed by strong ridges that are almost contiguous on the median line. There are no maxillary or vomerine teeth.

Glyphoglossus molossus Günther

(Fig. 12)

Glyphoglossus molossus Günther, Proc. Zool. Soc. London, 1868, p. 483, pl. 38, fig. 1 (type locality, Pegu).

The strongly truncate snout of this curious burrowing frog differentiates it from most of the Microhylidae, which are characterized, for the most part by narrow, somewhat pointed snouts. Their eyes

are diminutive, their length less than the distance between the eye and the tip of the snout. However, the upper eyelid is relatively heavy, overhanging and overlapping the lower. The head itself is strongly convex above, the occipital region highest, sloping gradually to the tip of the snout, the median line actually higher than the

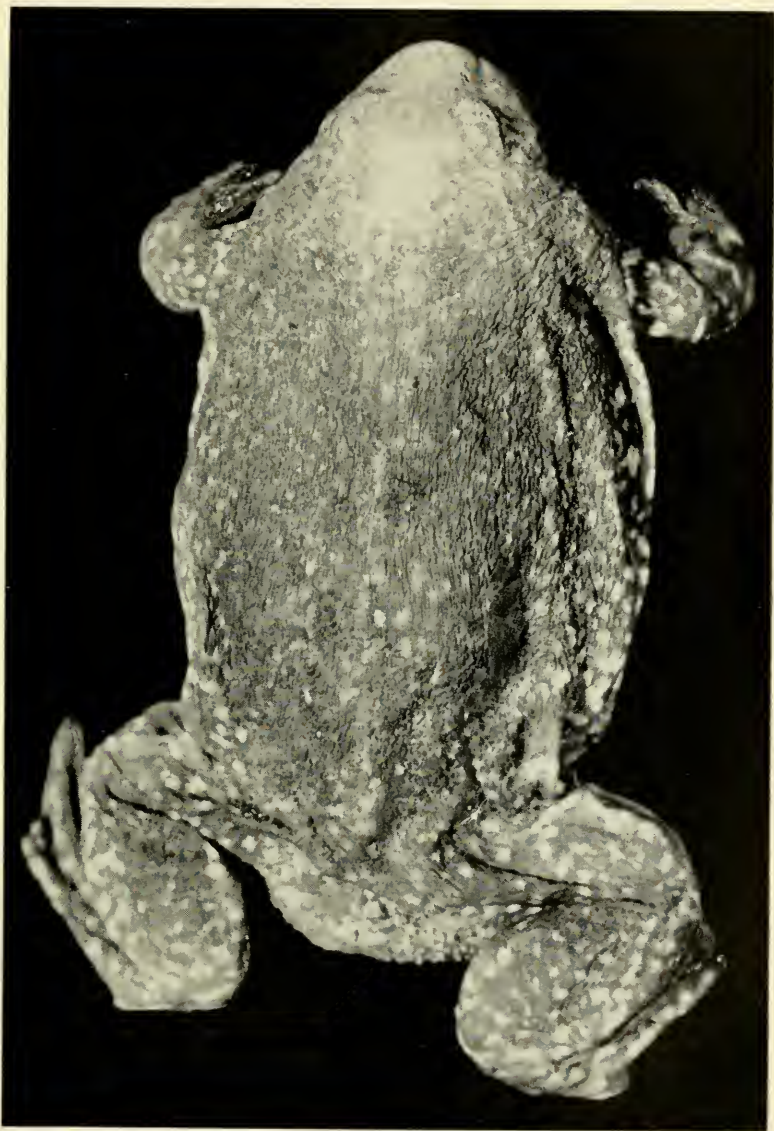


FIG. 12. *Glyphoglossus molossus* Günther. KUMNH No. 40018 "Thailand."
Actual snout-vent length, 73 mm.

eyes. Both upper and lower jaws are truncate, giving the head a very blunt appearance. A rather dim fold crosses the head just behind the eyes and reaches down to the mouth angle. The choanae are diagonally elongate, partly divided by a fleshy process from the anterior edge. While vomerine teeth are absent there are two small bony bolitoid processes behind, but slightly internal to the choanae, resembling vomerine teeth. A rounded median papule lies immediately in front of, and contiguous with the broad transverse fold lying across the palate some distance in front of the oesophageal opening. The tongue is peculiar. It is somewhat rounded behind with a suggestion of an anterior notch, and on each side a thickening leaving a median depression. The thickenings narrow posteriorly, leaving two diverging fingerlike ridges that fail to reach the back edge of the tongue. The posterior part of the tongue is free for a little less than a fourth of its length. Openings of the Eustachian tubes are large and circular. The vocal sac in the males is evidenced by two slitlike openings, one on each side of the tongue near the anterior part of the mouth. Externally, a transverse fold marks the position of the median vocal sac, which has two extensions running back above arm to shoulder.

The digits on the hand have lateral ridges (or fringes) along their inner edges, while between the second and third there is a tiny web remnant. There are four subarticular tubercles followed by three small tubercles on the metacarpals, and two large palmar tubercles, the outer elongate extending to the back border of the palm, the inner shorter and more distinct but larger than inner.

The toes, fully webbed, have their tips somewhat enlarged and thickened into small terminal pads. There are two or three subarticular tubercles on toes, except outer. A large sharp free-edged shovel represents the inner metatarsal tubercle; the small outer tubercle is approximated to first. When the limb is adpressed the anterior edge of the shovel reaches the tip of the snout.

The skin of face, snout, eyelids, anterior part of lower jaw, and lips covered with tiny firm rounded, sometimes subspinose tubercles. The body skin is wrinkled sometimes showing indistinct granulation. The rather smooth venter is neither granular nor areolate.

The entire body is discolored by rust and the preserving fluid.

Measurements in mm.: Snout to vent, 60; between nostrils, 5.3; arm, 31; leg, 81; foot, 36; shovel, 9; tibia, 25.

Remarks: The data have been drawn from KUMNH No. 33519 ♂ from Rat Buri, Thailand. A second specimen a female

containing ovarian eggs is without specific locality other than "Thailand." This specimen is somewhat larger and the sides and limbs are flecked and spotted with cream on a black-brown ground color. Both were collected by Dr. Boonsong Lekagul.

FAMILY BUFONIDAE

Bufo asper Gravenhorst

(Fig. 13)

Bufo asper Gravenhorst, Deliciae Musei Zoologici Vratislaviensis continens Chelonias et Batrachia, Fasc. 1. Lipsiae 1929, p. 58.

Two specimens of this large toad are present in the collection. These are KUMNH Nos. 40005 (BL 20125) and 40006 (BL 20039)



FIG. 13. *Bufo asper* Gravenhorst. EHT-HMS No. 30304, Km. 16 on Pahang Road, NW Kuala Lumpur, Selangor, Fed. Malay States. Actual snout-vent length, 80 mm.

both from Nakhon Si Thammarat, peninsular Thailand, Sept. 2, 1953, Dr. Boonsong Lekagul, coll.

The specimens are characterized as follows: a broad supraorbital ridge, often discernible with difficulty, and a short thick supratympanic ridge; snout short, bluntly oval, obliquely truncate; loreal region vertical, not or scarcely concave; interorbital region wider than an eyelid; tympanum small, distinct; fingers free, toes completely webbed, the digital tips widened; a strong inner tarsal ridge and two metatarsal tubercles, the inner largest. Tibiotarsal articulation reaches to eye; upper surfaces of body with rough, pyramidlike pustules and tubercles; parotid glands small but prominent.

Nearly uniform blackish brown; some light flecks on upper lip and under thighs.

The specimen figured is from Kuala Lumpur somewhat south of the Thai border. The species reaches a length of 215 mm.

Bufo melanostictus Schneider

Bufo melanostictus Schneider, *Historiae amphibiorum naturalis et literariae*. . . fasc. primus, 1799, p. 216 (type locality, "ex India orientali").

This common and widespread toad is represented by numerous specimens in the collection. The following localities are represented: EHT-HMS Nos. 31740-41 (RE 3946), Phu Kho (mt.), 522 m. elev., Kan Luang (village), Na Kae (district), Nakhon Phanon (province), R. E. Elbel and Dr. B. Lekagul colls., July 28, 1954; Nos. 31742-43 (RE 4261), Ban Nong Wai (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, Nov. 15, 1954, approximately 1780 m. elev., (same range as Phu Nam Lang (mt.) R. E. Elbel coll.; No. 31744 (RE 3833), Phu Phan (mt.), Sakon Nakhon (district), Sakon Nakhon (province), Thailand, July 2, 1954, elev. 550 m., Dr. B. Lekagul and R. E. Elbel, colls.; Nos. 31745-46 (RE 4030), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, elev. *circa* 1780 m. (in same range of mountains as Phu Nam Lang (mt.) but farther north,) Sept. 30, 1954, R. E. Elbel, coll.

Two other specimens from Thailand are without locality data, the tags having been lost. One measures 102 mm. snout to vent. The specimen is a female, the ovaries filled with small ovarian eggs and a stomach packed with wingless termites.

FAMILY PELOBATIDAE

Eight species representative of this family have been reported from Thailand as follows: *Megophrys nasuta* (Schlegel), *M. longipes* (Boulenger), *M. aceras* (Boulenger), *M. pelodytoides* (Boulenger), *M. carinense* (Boulenger), *M. feae* (Boulenger), *M. hasselti hasselti* (Tschudi), and *M. monticola* Günther.

Megophrys hasselti hasselti (Müller)

(Fig. 14)

Leptobrachium hasselti Müller in Tschudi, Classification der Batrachier, . . . 1838, p. 81, (attributed to Müller MS) (type locality, Java).

Two specimens, a male, EHT-HMS No. 31762 (RE 4078), and a dried female, 31763 (RE 4078), from Ban Na Muang (subvillage), Na Hao (village), Dan Sai (district), Loei (province), Thailand, Oct. 4, 1954, R. E. Elbel, coll.

Diagnosis: Head as wide or wider than body; canthus rostralis sharp; arms and legs weak, slender, the tibiotarsal articulation not reaching eye; no palpebral appendages; no vomerine teeth; two moderate palmar tubercles; one metatarsal tubercle, the outer tubercle missing vertebrae procoelous.

Description: Head as wide as long, the canthus sharp, terminating at nostril; nostril a little nearer eye than median point on lip; loreal region sloping, somewhat concave; snout in front of nostrils sloping obliquely; interorbital distance once to once and a half the width of an upper eyelid, and a third greater than distance between nostrils; tympanum rather small, its diameter less than half the length of eye-opening, the upper part covered by a sinuous fold from eye to angle of jaws. Eyes prominent.

Posterior two thirds of the tongue free, notched behind; two large slitlike openings to the vocal sac far back near mouth angle; choanae large; no vomerine teeth; openings of the palatal glands two, lying between inner level of choanae, but slightly in advance of the choanae.

Skin on dorsum minutely granular or pustular, the pustules larger and more prominent on sides; chin with small granules; entire venter with larger granules or areolations; underside of thighs smooth except for a few proximal scattered granules; a few granules about vent; a more or less distinct fold on the side, anteriorly touching, but not continuous with the supratympanic fold.

Arm small, slender; first finger a little longer than second, latter a little longer than fourth; small subterminal pads but no sub-

articular tubercles; undersurface of digits with some broken elongate ridges or callous areas that may incorporate the tubercles; inner fingers and inner edge of outer fingers with a narrow fringe or ridge, but no web; two prominent palmar tubercles; toes short, one-



FIG. 14. *Megophrys hasselti hasselti* (Müller). EHT-HMS No. 31762 Ban Na Muang, Na Haeo (village), Dan Sai (district), Loei (province), Thailand. Actual snout-vent length, 46 mm.

third to one-half webbed on inner toes but continued as a fringe or ridge to the terminal pad. A well-defined inner metacarpal tubercle; no outer tubercle; no tarsal fold or ridge; when limbs are folded at right angles to body the heels fail to meet; an elongate ridge on underside of the third and fourth toes, indicated also on second toe.

Color in preservative: Above lavender with darker lavender or purplish; darker irregular spots on back and sides; a dark longitudinal interorbital line; loreal region and lip with three or four spots, a dark line from nostril to eye, and from eye along the supratympanic fold, widening on the tympanum; arms and legs banded dark lavender above. Belly and chin lighter (yellowish) with clouding of lavender, or numerous flecks of brown or lavender.

Measurements in mm.: Snout to vent, 46; head width, 21.5; head length, 21.5; arm, 29; leg, 49; tibia, 16.5; foot and tarsus, 22.

Remarks: A second specimen is badly dried. It measures 60 mm. snout to vent.

Megophrys aceras (Boulenger)

Megalophrys montana aceras Boulenger, Fascic. Malay. Zool., I, 1903, p. 131 (type locality, Malay Peninsula).

One specimen examined—No. 20113 without a definite Thai locality. Very probably the specimen is from Nakhon Si Thammarat, collected by Dr. Boonsong Lekagul.

CLASS REPTILIA

ORDER TESTUDINES

FAMILY PLATYSTERNIDAE

Platysternon megacephalum Gray

(Fig. 15)

Platysternon megacephalum Gray, Proc. Zool. Soc. London, 1831, p. 107; and Illustrations of Indian Zoology, vol. 2, 1834, p. 62 (type locality, south China).

A single young specimen from Thailand has lost its tag and is of uncertain provenance. However, it is practically certain that it came from Dan Sai (district), Loei (province). The species may be diagnosed by the following characters: a blunt median dorsal keel not or but lightly notched; costal plates each with a tubercular keel. Nuchal scales very small; five vertebrals wider than costals; five costals, the three posterior smaller than largest marginals; twelve marginals on each side; serrate behind. Head large; tail elongate, covered with shields as follows: 28 paired subcaudals + 3 single scales; a dorsal series of 28 widened scales each with a median dorsal keel except three or four at base; the terminal scute is compressed, equally as long as the five preceding scales; the dorsal series of scutes separated from the subcaudals by an intercalated series on the base of the tail extending to the eighth pair of subcaudals; two or three intercalated scales on sides of elongate dorsal terminal scute.

Plastron small with six paired plastral elements and a very small median scale (abnormal?) between the gulars and humerals; bridge of plastron narrow, separated from marginals by three or four inframarginals.

Length of carapace, 50; width of carapace, 44; tail, 52.

Olive brown above with some black spots on the vertebral keels

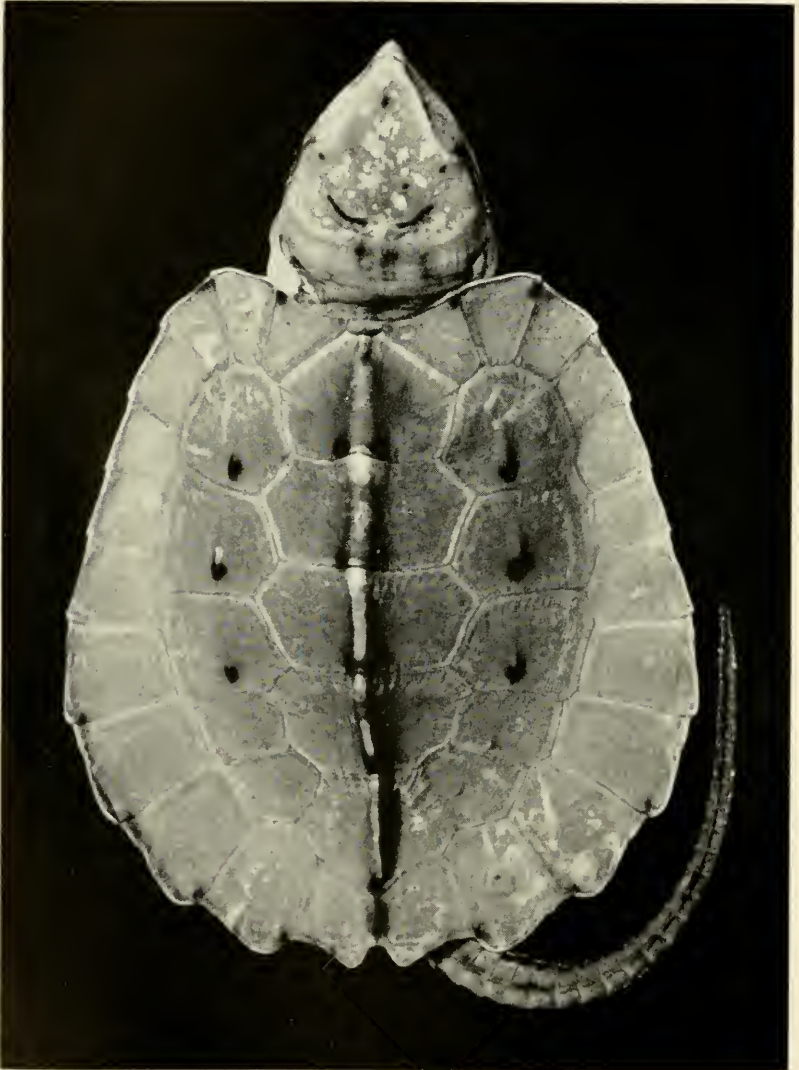


FIG. 15. *Platysternon megacephalum* Gray. KUMNH No. 40084, Thailand. Actual width of carapace, 44 mm.; greatest length, 50 mm.

and costal keels; blackish spots on anterior costal keels (see figure).

This species is an inhabitant of mountain streams and is said to be a tree climber!

ORDER CROCODYLIA

FAMILY CROCODYLIDAE

Crocodylus siamensis Schneider

Crocodylus siamensis Schneider, *Historiae Amphibiorum naturalis et literariae*, Fasc. II, 1801, p. 157 (type locality, Siam, based on drawings, *vide* M. Smith).

One typical young specimen (KUMNH 40085 [RE 784]) is in the collection from Bung Boraphet (lake), Nakhon Sawan (district and province), Thailand, collected by Robert E. Elbel Feb. 6, 1953.

This species may be distinguished rather readily from *Crocodylus palustris*, by having only four maxillary teeth instead of five (all visible from the outside of the closed mouth); from *Crocodylus porosus* by a shorter snout and in having the rows of bony dorsal plates in direct contact instead of having the bony parts separated by soft skin. In *siamensis* there are usually four (rarely two) postoccipital scutes, that are normally absent in *porosus*.

ORDER SQUAMATA

SUBORDER SAURIA

FAMILY GEKKONIDAE

Cyrtodactylus intermedius * (Smith)

Gymnodactylus intermedius Smith, *Jour. Nat. Hist. Soc. Siam*, 1917, p. 221 (type locality, Khao Sebab, SE Siam); *The fauna of British India including Ceylon and Burma; Reptilia and Amphibia*, vol. 2, Sauria, 1935, pp. 44-45, pl. 1, fig. 1.

A specimen of this species from Phatthalung, Thailand, was examined in the collection of Dr. Boonsong Lekagul. It is a female and while agreeing in color markings it lacks the preanal pores of the male. There is, however, a long series of enlarged femoral scales extending most of the length of the femur. The essential characters of the form are: male with a wide-angled series of preanal pores, a group of enlarged preanal scales and a series of six to ten enlarged femoral scales; eleven to twelve supralabials and nine to ten infralabials; a lateral fold of slightly enlarged scales; belly with 40 to 50 scales between folds. Body covered with large

* This species formerly was associated with *Gymnodactylus*. Garth Underwood, *Proc. Zool. Soc. London*, vol. 124, pt. 3, 1954, p. 475, revives the generic name *Cyrtodactylus* Gray with the type species *C. pulchellus*, restricting *Gymnodactylus*, *sensu strictu* to South America.

trihedral tubercles separated by small granules; tail with flat scales and whorls of larger tubercles, while there are transversely enlarged plates on underside. Grayish or brownish with blackish-brown cream-edged bands across back, the one on the neck reaching to eyes; tail banded.

Hemidactylus frenatus Schlegel

Hemidactylus frenatus Schlegel in Duméril and Bibron, *Erpétologie Générale* . . . , vol. 3, 1836, p. 366 (type locality, Java).

The following specimens obtained by Robert E. Elbel are in the collections: EHT-HMS Nos. 31830-31834 (RE 4971), Phu Phak Khi Nak (mt.), near Ban Nam Yen (subvillage), Kok Sathon (village), Dan Sai (district), Loei (province), approximately 1300 m. elev., between the ranges of Phu Nam Lang and Phu Lom Lo (mts.), Mar. 18, 1955; and No. 31835 (RE 3985), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, approx. 1780 m., in same range as Phu Nam Lang (mt.), Sept. 25, 1954.

KUMNH No. 31428 (RE 640), Banpong (city and district), Rat Buri (province), Thailand, Apr. 12, 1952; No. 31411, Banpong (city and district), Rat Buri (province), Feb. 29, 1952; No. 40086 (RE 914), Ban Lat (subvillage), Ban Kaeng (village), Phukhieo (district), Chaiyaphum (province), Thailand, Dec. 16, 1952, all collected by Robert E. Elbel.

Cosymbotus platyurus (Schneider)

Stellio platyurus Schneider, *Amphib. Physiol.*, vol. 2, 1792, p. 30, (type locality, unknown).

A series of specimens of *Cosymbotus platyurus* KUMNH Nos. 31413-31427 (RE 613, 619, 746) are all from Banpong (city), Banpong (district), Rat Buri (province), collected by Robert E. Elbel, Apr. 5, Apr. 8, and June 18, 1952, respectively.

Peropus mutilatus Wiegmann

Peropus mutilatus Wiegmann, *Nova Acta Acad. Leopold-Carol.*, vol. 17, 1835, p. 238 (type locality, Manila, P. I.).

Four specimens of this species collected by Robert E. Elbel are in the collection. These are EHT-HMS No. 31829 (RE 4575) from Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand; No. 31409 (RE 1085), Khorat (city and province), Thailand, Sept. 10, 1952; No. 31410, Banpong (city and district), Rat Buri (province), Thailand, Feb. 29, 1952.

Gekko gekko (Linnaeus)

Lacerta gekko Linnaeus, *Systema Naturae*, 10th ed., 1758, p. 205 (type locality, "habitat in Indies").

The following specimens are in the collections: EHT-HMS Nos. 31822-31823 (RE 4079), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, Oct. 4, 1954, R. E. Elbel, coll. and EHT-HMS Nos. 31824, 31825 (RE 5297), Phu Namlang (mt.), 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, May 23, 1955, Robert E. Elbel, coll.; KUMNH No. 33518 (BL 20024), Khao Khansong, Sriracha, Chon Buri, Thailand, July 15, 1953, Dr. Boonsong Lekagul, coll.; and No. 40020 (BL 20024), Ubon, Thailand, Nov. 9, 1953, Dr. Boonsong Lekagul, collector.

This very widely distributed species is easily recognized by its bluish (or ultramarine) to lavender color with numerous rusty-red spots on both upper and ventral surfaces. The first specimen, No. 31822, is the largest we have seen and doubtless is near the maximum size.

The two largest specimens, Nos. 31822, 31823, have the following measurements (in mm.) respectively: snout to vent, 185, 176; tail, 179, 150; total length, 364, 326; head width, 47, 42; head length, 54, 52; snout to arm insertion, 62, 60. The femoral pores are, 10-11, 12-11.

FAMILY AGAMIDAE

Genus *DRACO* Linnaeus

Within the territory of Thailand there are more species of these unusual gliding lizards of the genus *Draco*, than in any other area of equal size. In the extreme southern part of peninsular Thailand, south of the Isthmus of Kra, Thailand shares with the Federated Malay States many species which have a distribution extending into Indonesia, some even into the western Philippines. There are certain other forms that seem to have developed in continental Asia that occur in the mainland area of Thailand and extend varying distances down into the peninsula. Thus from the mainland we have *Draco maculatus* Gray, *D. haasei* Boettger, *D. whiteheadi* Boulenger, *D. divergens* Taylor, and *D. taeniopterus* Günther. Species presumably confined to the southern peninsular area and the Indonesian-Philippine region are *Draco quinquefasciatus* Gray, *D. colans* Linnaeus, *D. punctatus* Boulenger, *D. cyanolaemus* Boulenger, *D. blanfordi* Boulenger, *D. formosus* Boulenger, *D. micro-*

lepis Boulenger, *D. melanopogon* Boulenger. Another species with an Indonesian distribution, *D. fimbriatus* Kuhl, has been reported by Taylor (1934) from Chiang Mai, Thailand. One might suspect that still other species from the south have already found their way farther into northern continental territory. Malcolm Smith (1930) has suggested the need of more distributional data on these forms in Thailand. We would further suggest the need for larger series from everywhere so as to ascertain the amount of variation that may be expected.

The group, consisting of *maculatus*, type locality unknown; *divergens*, type locality, Chiang Mai, northern Thailand; *haasei*, Chantaboon, southeastern Thailand; *whiteheadi*, Hainan Island—may represent only subspecies of a single species. Until their distribution and variation is better known, we propose to maintain them as separate species. Günther's (1864) figure of *maculatus* is of a specimen from the coastal area of Thailand. Malcolm Smith suggests "Penang" as the type locality. If the type characteristics of the type specimens of *maculatus* can be found in a population from Thailand or Malaya, the type locality should be fixed so that the species or subspecies may be placed properly and referred to under the correct name. If this cannot be done a locality must be fixed arbitrarily.

The following key should be helpful in ascertaining identities of these interesting lizards.

KEY TO THAILAND SPECIES OF THE GENUS DRACO

- | | |
|--|---|
| 1. Tympanum sealy | 2 |
| Tympanum naked, lacking a covering of scales | 6 |
| 2. Larger (to 105 mm. snout to vent); nostril directed upward; no compressed spine on the supraciliary edge; wing membranes red with a series of five curving blackish bands, each as wide as the red interspaces; black band across the neck behind the dewlap, <i>quinquefasciatus</i> | |
| Smaller (to 85 mm. snout-vent length); nostril lateral directed outward; a small compressed spine on supraciliary edge | 3 |
| 3. A blue spot on each side of base of gular appendage (dewlap) | 4 |
| No blue spot on each side of base of dewlap | 5 |
| 4. No distinct row of lateral, conical, or trihedral nuchal scales; a row of trihedral scales, widely spaced on the base of the wing membrane; lateral nuchal expansion ("wattles") covered above with scales larger than largest dorsals, which are twice size of ventrals; base of dewlap orange without blue marks. Coppery red above with metallic reflections and black spots; on wings, orange with rounded dots on proximal half; head scales large, flat, with no or with few indistinct keels; usually a low nuchal crest of eight scales . . . <i>haasei</i> | |

Nostril pointing directly outward; dewlap tapering gradually to a fine point, blackish on anterior part, blue at the end, red behind the base; no lateral blue marks on each side; upper head scales strongly keeled; 8-9 supralabials; on each side of back a series of enlarged keeled dorsal scales; hind limb reaches halfway between elbow and axilla; wing reddish brown above with dark bars and small black spots; immaculate beneath. *whiteheadi*

5. Nostril pointing directly outward; upper head scales strongly keeled; no series of trihedral scales on side of neck, but a series along the base of the wing membranes; scales on lateral nuchal expansion about as large as largest dorsal scales; gular appendage often twice as long as head; dorsal scales but little larger than ventrals; wing membranes orange with scattered black spots rather uniform in size; wing membrane yellow below with one or two black spots; dewlap yellowish, with blue spots at base *maculatus*

Nostril directed outward and somewhat upward; head and neck prominently marked with black paired spots or transverse bars; spotting of wing membrane largely confined to proximal part, not arranged in rows; underside of yellow wing membrane much spotted with black; a nuchal crest involving 25 scales; dewlap yellow with paired blue spots at base, the length more than one and a half times that of head; loreal region and labials forming a broad shelf; snout constricted behind nostrils; a row of trihedral scales from neck along sides of body at base of wing; no distinctly Y-shaped group of scales, but a median row of three connecting with a transverse curving row of larger scales on snout; low tail crest present *divergens*

6. Nasal scale lateral, the nostril directed outward 7
Nasal scale dorsal, the nasal directed upward; dewlap longer than head 10
7. No caudal crest evident 8
A low caudal crest present 9

8. Supralabials, 7-10, smooth, unkeeled; a Y-shaped series of scales on snout; small nuchal crest; dewlap much longer than head; snout usually equal to or shorter than diameter of orbit *volans*

Snout equals diameter of orbit; nostril directed outward and slightly upward; 8-10 strongly keeled labials; dewlap translucent, covered with large scales; no caudal crest; wing membranes edged with brick red and with four or more black bands spotted with white; throat bluish; dewlap yellow *cyanoaemus*

9. Supralabials, 10-13; small nuchal crest; nostril directed outward and slightly upward; upper head scales very small; snout longer than diameter of orbit; wing membranes dark brown with lighter lines; below dirty gray, immaculate, or with a few scattered spots; chin and throat bluish with a network enclosing white spots; dewlap red or salmon pink *fimbriatus*

Snout equals diameter of orbit; Y-shaped series of scales on snout; two conical, triangular or spinelike tubercles on end of supraciliary (orbital) edge; 10-11 upper labials feebly keeled; dewlap of male about as long as head or shorter; tail crest strong; back and head

- with large black dots; four blotches form a cross between shoulders; wings black streaked with whitish; uniform whitish below; dewlap and nuchal appendages bright chrome yellow... *punctatus*
10. Dewlap coal black; a transverse light orange or whitish band across neck connecting with color of underside of nuchals expansions; snout shorter than diameter of orbit; 11-15 supralabials; breast and belly usually with brown spots... *melanopogon* 11
- Not so marked..... 11
11. Smaller; snout-vent length less than 85 mm.; snout equal to or shorter than orbit..... 12
- Larger; 100-125 snout-vent length; snout longer than diameter of orbit..... 13
12. Snout shorter than orbit; dewlap not or but little longer than head; 11-14 supralabials; arm extended, the hand reaches beyond tip of snout; wing membranes with fine black ill-defined transverse bands; base of dewlap and underside of nuchal expansion purplish red, with a black spot at base of dewlap in males; head and body 80 mm. *microlepis*
- Snout equals diameter of orbit; 7-9 supralabials; dewlap with very large scales slightly longer than head, arm reaches well beyond snout; hind limb to axilla or shoulder wing membranes with five arched transverse black bands sometimes forked at base; head and body 75 mm. *taeniopterus*
13. Supralabials, 9-10 keeled; dewlap much longer than head, translucent, covered with large scales; slight nuchal fold; arm reaches much beyond tip of snout; wing membranes marbled with dark brown and with lighter spots and thin white lines; immaculate beneath; scarlet on underside of nuchal expansions..... *blanfordi*
- Snout as long as diameter of orbit; 9-11 keeled supralabials; dewlap a little longer or equal to head length; thin, translucent, covered with large scales; arm reaches much beyond snout; wing membranes olive, edged with maroon or crimson; five transverse bands of blackish mottling, often indistinct; throat maroon or crimson in male, dark green in female..... *formosus*

Draco whiteheadi Boulenger

Draco whiteheadi Boulenger, Proc. Zool. Soc. London, Nov. 1899, pp. 956-957, pl. 66, fig. 1 (type locality, Hainan Island); Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, Feb. 7, 1935, p. 140 (northern Siam).

Diagnosis: Nostril directed laterally, tympanum scaled; head small, the snout considerably longer than the diameter of the orbit; 8-9 supralabials; dewlap one and one-half times as long as head; dorsal scales a little larger than ventrals, obtusely keeled; arm reaches tip of snout; wing membranes brick red above with round black spots, immaculate below; dewlap blue at end, blackish in front, red at base; related to *D. maculatus* but with longer snout, etc.

Description of species: Head short, the snout slightly shorter than the diameter of the orbit; rostral less than twice as long as wide, with eight glandular pits on front surface, bordered by two labials and five other scales; nasals craterlike, the nostril directed outward, separated from the rostral and labials by one row of scales; five or six scalerows separate the nasals; snout constricted behind nasals; a Y-shaped series of scales on snout, the basal part consisting of two large keeled scales, and the arms of two or three enlarged keeled scales reaching outward and backward; supra-orbital areas outlined by semicircular series of enlarged irregularly keeled scales that are separated mesially by three longitudinal series; outer row of supraoculars very large, keeled; one (or two) large keeled supraciliary scales extending half the length of the supraciliary border; on middle of the latter half of the border, a compressed triangular scale, and at the posterior border a large compressed tubercular one, flanked by one or two similar scales; six enlarged suboculars more or less continuous with a short series of three pyramidal scales, the last two largest; two or three irregular canthals; nine loreal series; supralabials ten, all with two to four pits; an enlarged triangular tubercle between scaled tympanum and angle of mouth; twin tubercles some distance back of tympanum, and another pair above and slightly posterior to tympanum; "occipital" scale narrow, elongate, flanked by groups of five enlarged irregular scales on each side; distal to each of the two groups and slightly posterior is a somewhat elevated group of about six irregular enlarged scales, separated from each other by four small or two enlarged scales; on nape at normal point for the beginning of a nuchal crest are two conical scales surrounded by eight scales, altogether forming a rosette. Infralabials 8-8, also bearing pits; mental unpitted, its border about equal to rostral border, touched behind by two labials and five scales; gular scales minute; male gular appendage (21 mm.) longer than head (14 mm.), covered on its distal half by large regular scales; lateral nuchal expansions relatively small, with larger scales above.

The nuchal crest is not or barely indicated; a series of large somewhat compressed pyramidal or trihedral scales begins on neck and curves up above arm, then follows along the base of the wing membrane to level of thighs, about 16 on neck anterior to wing, ten or eleven along wing base; a short indefinite row of similar scales higher up on shoulders; scales of the dorsal rows along back much larger than the small ventral keeled scales, keeled or smooth, often with their edges raised suggesting lateral keels. A

distinct caudal crest; a series of mucronate scales begin on the dorsal part of the tail separated at first by three scalerows from the caudal crest and more posteriorly comes to border the crest scales; another serrate series that begins on outer edge of the base of the tail comes later to border the two median ventral series, which have high keels. A fringe of enlarged scales along the posterior edge of thigh; front dorsal part of thigh and tibia with enlarged keeled scales; 27 lamellae under fourth toe; scales on breast, on dorsal part of upper arm, and on dorsal part of forearm, enlarged, keeled; posterior edge of forearm with a fringe of larger scales.

Color in preservative: Above brownish, reticulated or dotted with some lighter marks, and with deep black marks on head and neck; wing membranes light tan with black marbling or flecking, not forming bands or rows of spots; wing membrane below immaculate gray save for a narrow elongate curved black mark near outer border. Chin darker, speckled with lighter; breast flecked with brownish spots; tail gray, banded with darker to tip; dewlap blackish on anterior margins, remainder whitish, probably orange-red in life; along side of the base of the dewlap are black marks separating the light color of the underside of the lateral nuchal expansions from that of the dewlap area.

Measurements in mm.: Snout to vent, 64; tail, 102; length of head, 14; width of head, 10.5; height of head, 8.5; snout to orbit, 5; snout to tympanum, 12; axilla to groin, 33; arm, 27; leg, 33; length of gular appendage, 21; width of alar membrane, 22.

Remarks: Malcolm Smith (*loc. cit.*) has referred *D. whiteheadi* to the synonymy of *Draco maculatus* (Gray), but mentions the fact that specimens of this form occur in northern Thailand, Hainan and Tongking. The type is 86 mm. snout to vent, the tail, 148 mm.

Draco haasei Boettger

Draco haasei Boettger, Zool. Anz., no. 433, 1893, pp. 424-425 (type locality, "Pratchedli Kan Sabab Chantaboon," Siam).

Diagnosis: Related to *D. maculatus* Gray but the upper side of the lateral nuchal expansion covered with scales which are larger than the largest scales on the back, which in turn are twice the size of the belly scales; the base of the gular appendage is deep orange, without blue flecks.

Description of species: Head small. Snout a little longer than the diameter of the orbit. Nostril lateral, directed outwards. Tympanum scaled. Upper head scales large, weakly keeled. A pair of scales on the supraocular region distinctly enlarged, much larger

than the supralabials; a distinct compressed or conical scale in the beginning of the last third of the supraciliary arch and a second broader and shorter one at the end of the supraciliary region; eight supralabials; gular appendage of the male long, nearly twice head length, covered with scales which are somewhat larger than the belly scales. Upper side of lateral nuchal expansions covered with very large, strongly keeled scales, larger than supralabials and the largest back scales. A very short and low nuchal crest consisting of eight scales. Scales of the back irregular, of very dissimilar form and size, the largest reaching twice the size of the sharply keeled belly scales, and with obsolescent keels or lacking keels altogether. On each side of the back and especially distinct in the posterior part, is a row of large trihedral keeled scales separated rather widely. The arm when laid forward reaches well beyond the tip of the snout; the hind leg reaches the axilla.

Color: Above coppery red with metallic reflections and marked with blackish dots, those on the neck arranged symmetrically; a triangular black interorbital spot; wing membrane delicate orange color with whitish longitudinal lines and on the proximal half richly strewn with small round black spots. Underside unicolor and only on the anterior point of wing membrane one or two black spots. Underside of the head with brownish reticulation; lateral nuchal expansion below, deep orange lacking dark spots.

Total length, 178; head length, 14; head width, 11; rump length, 51; arm, 28; leg, 38; tail, 113; dewlap, 23.

The type locality is Chantaboon [Chanthaburi], Siam. It was taken on a tree trunk near the village of Pratchedi, Kan Sabab, [Khao Sabap (mt.)] together with *Draco taeniopterus* Günther. The species was collected by Dr. Eric Haase, Director of the Royal Siamese Museum in Bangkok, who at the same time collected the following specimens at Bangkok: *Lygosoma chalcides* Linnaeus, *Dryocalamus davidsoni* Blanford, *Rana tigerina* Daudin, *Microhyla inornata*.

[The above is a free translation of the type description.]

Draco maculatus (Gray)

Dracunculus maculatus Gray, Catalogue of the specimens of lizards in the collection of the British Museum, London, 1845, p. 236 (type locality, unknown).

Draco maculatus Günther, Reptiles of British India, 1864, p. 125, pl. 13, fig. C. (full drawing of a Siamese specimen. Also reports specimens from "Pinang" and Tenasserim); Smith, Bull. Raffles Mus., Singapore, Straits Settlements, no. 3, Apr. 1930, p. 21; Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. II Sauria, Feb. 7, 1935, pp. 138-140, fig. 42.

Diagnosis: Tympanum scaled; head scales large, partly keeled; nasal lateral, the nostril directed outward; gular appendage uniform orange, very long, with a blue spot on each side of the base. A series of rather flat enlarged scales forming a Y-shaped group on the snout.

Description of species: (from KUMNH No. 40043 [BL 20008], Nakhon Si Thammarat, peninsular Thailand), Dr. Boonsong Leka-gul coll. Head moderately large, the snout as long as the diameter of the orbit; nasal scales lateral, craterlike, the nostril directed outward; rostral about two and one-half times as wide as high, bordered by two labials and seven postrostrals; nasal separated from the rostral by one scale, from its fellow by five scalerows; a median row of three large somewhat elevated scales on snout; on each side of the most posterior is a row of three still larger scales which run outward and backward to the upper edge of the orbital rim; three canthal scales, the last forming part of rim of orbit, very large, dimly keeled, followed by two supraciliaries; a compressed scale on supraciliary border some distance behind the two; a knoblike scale at back of the supraciliary (orbital) edge; a rather indefinite row of scales form semicircles about upper supraocular areas, separated mesially by two or three scalerows; a partial row of four large supraoculars and another somewhat smaller row; occipital area somewhat inflated with two converging heavy keellike ridges on each side of the median occipital region; scales in occipital region large, irregular, the "occipital" usually one of the smaller ones; the keel crossing two large scales on each side; a slight nuchal crest involving 10-12 scales; supralabials, 8-10; four or five slightly enlarged suboculars separated from the labials by two scalerows; three or four larger postoculars continuous with a series of three large scales running back from eye on the temporal region, the last somewhat pyramidal; a larger moundlike scale on anterior border of scaled tympanum; a few flat enlarged scales in upper temporal area, slightly craterlike; a compressed tubercular scale some distance above and a group of three a little behind the tympanum; mental bordered by two labials and five postmental scales; one or two enlarged scales along side of neck; smooth or slightly keeled dorsal scales nearly equal to the ventrals which are strongly keeled; a row of enlarged keeled trihedral scales along base of wing membranes; scales on top of nuchal expansion keeled, larger than dorsals; on under surface a patch of scales with edges curiously crenulated; dewlap elongate, the distal part covered with large imbricating smooth scales; an indistinct or low dorsal crest; scales on breast, on

dorsum of upper arm and forearm, on anterior dorsal part of thigh and lower leg, enlarged, keeled; a distinct fringe of large scales bordering posterior side of leg and outer edge of forearm. The keeling on the tail, owing to its preservation, is difficult to describe (scales soft and flattened); wing membrane ample; leg reaches a little more than halfway from elbow to axilla; arm brought forward the fingers extend beyond tip of snout.

Coloration: Gray to ultramarine with indefinite darker head marking; the sides of neck and back flecked or reticulated dimly with darker gray; wing membrane flesh color (reddish or orange in life) with very numerous brown or blackish spots or short bars forming indistinct irregular transverse rows, and longitudinal rows, the latter indistinctly connected by fine whitish lines; wing membranes gray, immaculate below; tail banded with darker; hind leg with one or two lighter bands.

Measurements in mm.: Length, snout to vent, 82; tail, 126; head length, 17; head width, 11; snout to tympanum, 14.5; snout to arm insertion, 31; axilla to groin, 45; dewlap, 27; arm, 33; leg, 40.

Remarks: Two females, KUMNH Nos. 40044 (BL 20106) and 40045 (BL 20109), Dr. Boonsong Lekagul collector, are from Thailand. The tags have disintegrated but they are most probably from Nakhon Si Thammarat. They cannot be associated certainly with any particular species having a scaled tympanum. The wing membranes are somewhat reddish or pinkish, the black coloration forming five or six transverse lines, the spots strongly confluent. The gular areas are probably uniform light orange in life; the dewlap is short but distinct. While the dorsal nuchal crest is absent, one specimen has a row of three larger median scales just back of the occipital region. The caudal crest is wanting but the small occipital ridges or keels are present. These may represent a subspecific form as yet unrecognized.

Two specimens, EHT-HMS Nos. 31789 (RE 4971) and 31790 (RE 4971) are seemingly typical. They were taken from Phu Phak Khi Nak (mt.), approx. 1300 m. elev., between Phu Nam Lang and Phu Lom Lo (mts.) near Ban Nam Yen (subvillage), Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, Mar. 18, 1955, R. E. Elbel, collector.

Draco blanfordi Boulenger

Draco major (nec Laurenti) Blanford, Jour. Asiat. Soc. Bengal, vol. 47, 1878, p. 125 (type locality, forest east of "Tavoy, India").

Draco blanfordi Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 267, pl. 20 (head); Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 141-142, fig. 41, B.

Two specimens are in the collections, KUMNH Nos. 40042, 40097. The first has the following characters:

Rostral bordered by seven scales; nasal large, separated from rostral by a single scale; snout about as long as the diameter of the orbit; nostril in craterlike nasal, directed upward; tympanum not covered with scales; scales on head rugose, keeled or ridged, especially on frontal and snout region; a longitudinal ridge on anterior frontal region consisting of three or four large scales; on each side of this the scalerows from the snout curve outward; at posterior end of the ridge the keels of the scales are transverse or curve outward and backward; a semicircular scalerow of larger scales outlines the orbit above, anteriorly bearing high keels directed outward; these two series separated mesially by three scalerows; supraoculars variable in size but eight or ten are larger than the rest, all bearing low keels; "pineal" eye in a tiny scale between a pair of larger scales; supralabials, 9-11; infralabials, 10-11; edges of lips with very numerous small well-defined pits, which represent gland openings; three or four irregular canthal scales; a large tubercle at posterior corner of eye; a row of three scales behind eye, the last largest; two rows of enlarged subgular scales behind mental separated from the labials; lateral nuchal expansion ample, the outer scales both above and below enlarged; gular appendage (dewlap) longer than head, translucent, the tip rounded, covered with scales larger than ventral scales. Dorsal scales somewhat irregular, smooth or slightly keeled; a faint trace of a nuchal crest; ventrals larger than dorsals, with strong keels; an irregular row of enlarged scales or groups of scales along side near base of wing membranes. Tail strongly compressed with a slight caudal crest and a ventrolateral row of micro-nate scales; undersurface of the tail with two rows of very heavily keeled scales. Arm brought forward, the hand extends beyond the snout; leg brought forward, the longest toe reaches to about halfway between the elbow and arm insertion. The wing membranes are ample, supported by four elongate ribs, and two short ribs anteriorly; a slight webbing on back of leg, fringed with enlarged serrate scales; 28 lamellae under longest toe.

Color in preservative: Generally brown or gray brown; head grayish, the upper orbital area outlined in dark brown; a median dark spot between eyes; a pair of occipital dark spots; upper nuchal region with several small dark flecks; when wing membranes are stretched under water very dim longitudinal discontinuous lines of brown can be discerned on the dorsal surface; below uniform gray

somewhat darker near anterior border (probably yellowish in life); dewlap whitish, possibly yellow in life; blackish areas on sides of neck, and a cream area under the nuchal expansion; back nearly uniform gray-brown without distinct banding or mottling; tail not banded, lighter than body.

Measurements in mm.: Length, snout to vent, 127; tail, regenerated, 117; snout to eye, 10; snout to auricular opening, 23; snout to arm insertion, 38.5; axilla to groin, 67; arm, 52; leg, 65.

Remarks: The single described specimen is No. 40042 from Nakhon Si Thammarat, Thailand, collected by Dr. Boonsong Lekagul. The species is regarded as rare but it probably ranges over most of the country. It has been obtained chiefly in peninsular Thailand.

The second specimen of this species in the collection is No. 40097 (RE 1433), from Hinlaem (village), Trakhanun (district), Kanachanaburi (province), Thailand, Nov. 6, 1952. Robert E. Elbel and H. G. Deignan, collectors. This preserved specimen shows the color as bluish gray-green with some metallic reflection. The wing membranes are light brown, lined with narrow whitish streaks (in No. 40042 the white has disappeared leaving the brown color appearing as dim narrow stripes; when held to the light the membrane is translucent and the white streaks above are visible through the wing). Venter light, lighter than the underside of the wing membrane. There is some evidence of mottling under the chin. The dewlap is creamy in color and semitransparent; there are large cream-white areas on underside of the nuchal expansions.

Somewhat above each tympanum is an enlarged pointed tubercular scale. Most of the characters listed for No. 40042 likewise apply to this second specimen.

Draco melanopogon Boulenger

Draco melanopogon Boulenger, Catalogue of the Lizards in the British Museum, vol. 3, 1887, p. 492 (type locality, Malacca); Laidlaw, Proc. Zool. Soc. 1901, pt. 1, p. 307; Boulenger, Fascic. Malay Zool., vol. 1, 1903, p. 152; and A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra, to Singapore including the adjacent islands; Reptilia and Batrachia, 1912, pp. 62-63; Smith, Bull. Raffles Mus., No. 3, April 1930.
Draco nigriappendiculata Bartlett, Crocodiles and Lizards of Borneo, 1895, p. 82.

Diagnosis: This species is characterized by a small head, the snout shorter than the diameter of the orbit; tympanum distinct, not covered with scales; nostrils in craterlike scales, the openings directed upward and slightly backward; scales on latter two thirds of the supraciliary border not enlarged or specialized; arm as long as leg or nearly so; no Y-shaped grouping of enlarged scales on

top of snout; no trace of a nuchal crest; a narrow groove between the elevated orbits on midline of head. The gular appendage (dewlap) is a deep black color.

Description of species: (KUMNH No. 40047). Head relatively small; the snout slightly shorter than diameter of orbit, the frontal region declivous, the area between nostrils flattened; five scales between nasals; rostral about four times as wide as high, bordered by two labials and nine postrostrals; nasal high, craterlike, separated from rostral by one scale, nostril directed upward and somewhat backward; scales on snout small, subequal; the scales on the front edge of the bony orbit including canthals and anterior supraciliaries are elongate, heavily keeled, the scales standing nearly vertical. Supraorbital region strongly elevated, the outer supraoculars only slightly larger than other scales, the semicircular scale series not differentiated clearly; a deep groove between orbits; occipital region somewhat inflated, the scales larger than the supraoculars but very unequal in size; "occipital" with a distinct "eye spot," as large as any surrounding scales; supralabials, 12-13, each with a median longitudinal ridge, keel, or series of tubercles, the lower edges slightly elevated; infralabials, 12-13, each with two longitudinal ridges; mental subtriangular, as wide as rostral, bordered by two labials and four or five scales, the outer largest; no distinguishable rows of enlarged gulars; an indistinct rounded tubercle at extreme posterior part of the supraciliary edge on the orbital rim; no trace of a nuchal crest; wing membrane ample; a row of about seven large distinct keeled scales along basal border of membrane; scales on the nuchal expansions enlarged above and below near outer edge; gular appendage of the male elongate, narrowed towards tip. Arm brought forward, the anterior fourth of forearm and hand reach beyond snout; leg laid forward, the toes reach the axilla; a narrow web, or fringe, bordering the posterior border of the hind leg, is edged with a series of broadened scales; tail long, without crest, but at base on each side is a row of larger scales forming a flaring serrate edge; dorsal body scales small, subequal, feebly keeled or smooth, smaller than scales on ventral surfaces; very numerous glandular pits in scales or membranes within mouth near edge of lip.

Color: Generally brownish above on body; wing membranes dark blackish brown with rows of small white (yellow in life) spots that form both indefinite longitudinal and transverse rows; no markings on underside of wing membranes; breast and ventral surfaces with small brown spots. Chin, underside of neck, and

arms with some brownish flecks. Head rather light brown. Dorsum of neck and body with lighter yellowish or whitish flecks or markings. Underside of hind legs and under tail whitish (yellowish).

Measurements in mm.: KUMNH No. 40047 Phatthalung, Thailand, Sept. 15, 1954; No. 40048 Ban Chawang (village), Chawang (district), Nakhon Si Thammarat (province), Thailand, Mar. 1954; No. 40049 (exact locality uncertain), 1953, respectively: length, snout to vent, 80, 82, 73; tail, 91 (R), 153, 146; snout to orbit, 4, 4.5, 3.8; snout to ear, 10, 10, 10.3; snout to arm insertion, 28.5, 28, 25; axilla to groin, 48, 48, 41; height of head, 8, 8, 7; arm, 42, 43, 37; leg, 41, 45, 42.

Remarks: These three male specimens are the only ones in the collection; they agree very well in markings and general characteristics. However, there appears to be some variation in the length of the snout, the gular area of females is gray, and the arm is as long as or longer than the leg.

Goniocephalus * *armatus armatus* ** Gray

Agama armata Gray, Zool. Jour., vol. 3, 1827, p. 216 (type locality, Singapore).

Acanthosaura armata Boulenger, Catalogue of the lizards in the British Museum, vol. 1, 1885, p. 301, pl. 22, fig. 1.

Goniocephalus armatus arma.us M. Smith, Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, Feb. 7, 1935, pp. 157-160.

Although certain adult characters are not now evident, two juvenile specimens, from Phatthalung (district and province), largely on the basis of geographic probability, are assigned to this subspecies. They are KUMNH Nos. 40053, 40054. They were collected by Dr. Boonsong Lekagul, Sept. 15 and Nov. 1, 1954.

Goniocephalus armatus crucigerus (Boulenger)

Acanthosaura crucigera Boulenger, Catalogue of the lizards of the British Museum, vol. 1, 1885, p. 302, pl. 22, fig. 2 (type locality, Tavoy, Tenasserim).

Goniocephalus armatus crucigerus M. Smith, Fauna of British India, including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 160-161, fig. 49.

The following specimens are in the collections: EHT-HMS No. 31645 (RE 5240), Ban Bo (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, May 15, 1955, R. E. Elbel, coll., ("in the range of Phu Nam Lang (mt.) but farther north,

* Kaup's original spelling was *Gonocephalus* (1825), but was corrected to *Goniocephalus* by him in 1827.

** *Acanthosaura* Gray. Malcolm Smith has synonymized that genus with *Goniocephalus* since he regards the postorbital spine as not being of generic importance. Until further studies are made we will follow this disposition of the species formerly in *Acanthosaura*.

elev. approx. 1780 m."); EHT-HMS Nos. 31714-16 (RE 3984), Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, approx. 1780 m. elev. ("range of Phu Nam Lang mt."), Sept. 25, 1954, R. E. Elbel, coll.; EHT-HMS Nos. 31708-31710, same data; EHT-HMS Nos. 31712-31713 (RE 5490) from Phu Nam Lang (mt.) 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, 1955, Robert E. Elbel, coll.; KUMNH Nos. 40099 ♀, 40010 ♀ (RE 1432-1434), Hin Laem (village), Tha Khanum (district), Kanchanaburi (province), Thailand, Nov. 3 and 6 (respectively), H. G. Deignan and Robert E. Elbel, collectors.

The two specimens from Kanchanaburi province are from a point about 135 km. east of the type locality but from a higher elevation. In these the nuchal crest is much higher than the dorsal crest (8 mm.-3 mm.). The postorbital and occipital spines measure four millimeters, while the length of the orbit is approximately nine millimeters. There is a faint suggestion of a gular pouch but since the specimens are soft the extent of the pouch cannot be accurately determined. The largest of these is 115 mm. snout to vent.

Specimens from Loei (province) in the collection have a rather typical color pattern. Most of them are subadult. Several show the tympanum scaled over more or less.

All the specimens have the nuchal crest separated from the dorsal crest and the scales of the series have broader bases than are indicated in Smith's figure (*loc. cit.*).

Two or three of the specimens have ovarian or oviductal eggs. Smith (p. 158 *loc. cit.*) states that ten or twelve eggs are laid, 12 x 20 mm. in size. The eggs are not spindle-shaped.

Genus CALOTES

Five species of the genus *Calotes* are well known in Thailand. One other, *Calotes microlepis* Boulenger, may also be present since it has been taken on both sides of the country in Tenasserim and Annam. The species may be distinguished by the following key:

KEY TO THE SPECIES OF CALOTES IN THAILAND

- | | |
|---|---------------------|
| 1. A part of the lateral scales point backwards and downwards; no fold in front of shoulder on neck | 2 |
| Scales on sides all pointing backwards and upwards | 4 |
| 2. The leg reaches at least to eye; ventral scales larger than dorsals; generally greenish in life | <i>cristatellus</i> |
| The leg fails to reach the eye | 3 |

3. Scales in 48-56 rows around body at middle; general color brownish in life; head slender *floweri*
Scales in 65-72 rows around body at middle; color brownish in life *microlepis*
4. No fold or pit in front of shoulder; two separated spines above tympanum *versicolor*
An oblique fold or triangular pit in front of shoulder covered with small granular scales 5
5. A postorbital spine; upper lip usually lacking a light stripe *emma*
No postorbital spine; usually a light labial stripe present, continued on neck some distance *mystaceus*

One curious character of many, if not all, of the species of this genus is the hairlike structures on the scales. The keels are usually present and at least over much of the body they are produced into spines or mucrones which may have a terminal or a lateral crater. From this craterlike region a very fine hair emerges which may attain a length of from .2 to .45 mm. in length. *In situ* the hair appears to emerge directly from under the mucrone, or if a mucrone is absent it may emerge from a small pit near the back of the scale.

Calotes floweri Boulenger

Calotes floweri Boulenger, Fauna of the Malay Peninsula . . . , 1912, p. 70 (type locality, Chantabun, SE Siam and Tunong Tahan, Malay Peninsula); Smith, Jour. Fed. Malay States Mus., vol. 10, 1922, p. 269; Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935; pp. 186-187.

Calotes microlepis (*nec* Boulenger) Boulenger, Jour. Fed. Malay States Mus., vol. 3, 1908, p. 66.

We propose to restrict the type locality of *Calotes floweri* * Boulenger to Chantabun = Chanthaburi, SE Thailand.

A single Thai specimen (EHT-HMS No. 31717) in our collection belongs to *Calotes floweri*. The specimen has lost its field tag and we are uncertain as to its exact provenance.

The head is relatively narrow, its length equal to twice its width. The frontal region is flat, and the distance from the edge of the orbit to the nostril is slightly greater than the diameter of the orbit. The rostral is wide and low, bordered behind by two labials and five postrostrals. Following these scales on the snout and frontal area there is a group of keeled scales arranged in a slender Y-shaped series, the scales forming the branches of the Y continuous with the two enlarged "semicircular" scale series on the inner borders of the supraocular region. The two semicircular series are separated by three scalerows. At the level of the occipital scale there is a

* Smith (*loc. cit.*) calls attention to certain differences between the northern (Indo-chinese) specimens and the southern (Malay) specimens.

transverse row of slightly elevated scales, and a few enlarged scales on each side of the occipital region. The scales covering the temporal regions are unequal with one irregular series from the eye to above the tympanum. The supralabials are twelve, the last three not clearly differentiated, the infralabials eleven. The mental is narrow, about as wide as long, followed by two enlarged rows of six scales each and separated from the labials (except first) and from each other by from one row of scales (anteriorly) to five rows of scales (posteriorly).

The lateral scales are arranged in more or less distinct transverse series, the scales pointing backward and downward. Dorsal scales are subequal in size or larger than those on the venter but the latter are more strongly keeled.

As is typical in *Calotes* the body is strongly compressed, the hind limbs slender, the gular pouch small or absent. The tail is definitely compressed, but swollen and serrate at its base, and the median dorsal scales somewhat larger than the rest. There are 64 scales in a transverse row around the body.

Four indefinite darker marks are present on the dorsum, the first between the shoulders. Radiating streaks from the eye are in evidence. The venter is light with or without dark marks. The tail is lighter than the body and barred with bands of brown and light tan.

Calotes versicolor (Daudin)

Agama versicolor Daudin, Histoire naturelle des Reptiles, vol. 3, 1802, pp. 395-397, pl. 44 (type locality not stated by Daudin).

Calotes versicolor M. Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935 (this is based on Kuhl's report). Malcolm Smith fixes the type locality as Pondicherry, India (may therefore be accepted as the "terra typica").

The specimens of *Calotes versicolor* in the collection are from the following localities:

KUMNH Nos. 31388 (RE 621), 31389 (RE 615), 31390 (RE 626), 31391 (RE 623), 31392 (RE 722), 31404 (RE 622), Banpong (city and district), Rat Buri (province), Thailand, Apr. 7-17, 1952; 31393 (RE 593), Latya (city), Latya (district), Kanchanaburi (province), Mar. 28, 1952; 31394 (RE 612), Ban Tham (village), Tamuang (district), Kanchanaburi (province), Apr. 5, 1952; 31395-31396 (RE 962), Khon San (village), Phukhieo (district), Chaiyaphum (province), Thailand, Dec. 24, 1952; all collected by R. E. Elbel.

KUMNH Nos. 40027 (BL 20009), 40028 (BL 20019), Nakhon Si Thammarat Sept. 1953; 40029 (BL 20096), Rayong, Sept. 21, 1954;

40030-32 (BL 20123) "Thailand"; 40033 (BL 20141), Mae Hong Son, Feb. 1955; 40034 (BL 20101), 40035 (BL 20102), 40036 (BL 20122), 40037 (BL 20124), 1954-55. Phatthalung; all collected by Dr. Boonsong Lekagul.

KUMNH Nos. 40089-90 (RE 3473), 40095 (RE 3551), Phu Lom Lo (mt.), 2100 m. Kok Sathon (village), Dan Sai (district), Loei (province), Mar. 26, and Mar. 31, 1954; 40092-94 (RE 3175), Khao Sawan (mt.), approx. 600 m. elev., Sieo (village), Loei (district and province), Thailand, Nov. 29, 1954; all collected by Robert E. Elbel, and Dr. Boonsong Lekagul.

Calotes emma Gray

Calotes emma Gray, Catalogue of the specimens of lizards in the collection of the British Museum, London, 1845, p. 244 (type locality, "Afghanistan"); M. Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, Feb. 7, 1935, pp. 195-197, fig. 55.

This widespread species probably occurs throughout Thailand wherever suitable forested country exists.

The scales, usually terminating in spines or mucrones, also have a small fine flexible hairlike projection growing out from a small cavity just below the terminal spine and extending farther than the spine. These are usually much finer than human hair and their length is from .4 to .45 mm. in length.

Specimens of *Calotes emma* in the collection are from the following localities: EHT-HMS Nos. 31667 (RE 5240), Ban Bo (subvillage), "in the range of Phu Nam Lang (mt.) but farther north," elev. approx. 1780 m., Na Haeo (village), Dan Sai (district), Loei (province), Thailand, May 15, 1955, Robert E. Elbel, coll.

Nos. 31674 (RE 3675), Phu Phan (mt.), 550 m., Sakon Nakhon (district and province), June 12, 1954.

Nos. 31675 (RE 3918), 31676 (RE 3918), 31677 (RE 3868), 31678 (RE 3868), Phu Kho (mt.), 522 m., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), July 17-25, 1954, Dr. Lekagul and Robert E. Elbel colls. No. 31679 (RE 4650), Phu Lom Lo (elev. 2100 m.), Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, Feb. 15, 1955, R. E. Elbel.

KUMNH Nos. 40087 (RE 3416), Bang Sang Kho (subvillage), Khok Phu (village), Sakon Nakhon (district and province), Thailand, Feb. 8, 1954; 40088 (RE 3175), Khao Sawan (mt.), 600 m. Sieo (village), Loei (district), Loei (province), Thailand, collected by Robert E. Elbel.

Nos. 40023 (BL 20077), 40024 (BL 20100), 40025 (BL 20125), Phatthalung (province), Thailand, 1954; 40026 (BL 20088), Ban

Chawang (village), Chawang (district), Nakhon Si Thammarat (province), Thailand, Mar. 1954. All collected by Dr. Boonsong Lekagul.

Calotes mystaceus Duméril and Bibron

Calotes mystaceus Duméril and Bibron, *Erpétologie Générale*, vol. 4, 1837, p. 408 (type locality, Burma); M. Smith, *The fauna of British India including Ceylon and Burma; Reptilia and Amphibia*, vol. 2, Sauria, Feb. 7, 1935, pp. 197-199.

This species is widely distributed in continental Thailand but appears to be absent in the peninsular part of the country. It reaches elevations up to and perhaps above 1500 m. elevation.

The specimens of *Calotes mystaceus* are from the following localities: KUMNH Nos. 31399 (RE 719), 31400 (RE 721), 31401 (RE 724), Lam Phaya (village), Nakhon Pathom (district and province), Thailand, Apr. 17-18, 1952, R. E. Elbel coll. No. 31402 (Y 197), Boekprai (village), Bangpong (district), Rat Buri (province), Thailand, May 30, 1952, R. E. Elbel coll. Nos. 31403 (RE 872), 31442 (RE 873), 31443 (RE 893), Non Khun (village), Phukhieo (district), Chaiyaphum (province), Thailand; Dec. 10, 13, 1952. R. E. Elbel, collector.

KUMNH 40038 (BL 20026), 40039 (BL 20026), Nakhon Pathom (province), Thailand, July 18, 1953, Dr. Boonsong Lekagul coll. No. 40040 (BL 20043), Nakhon Si Thammarat (province), Sept. 1953, Dr. Boonsong Lekagul coll.

Liolepis belliana belliana (Gray)

Uromastix belliana Gray, *Zool. Jour.*, vol. 3, 1827, p. 220 (type locality, Penang; based on a drawing by Major-General Thomas Hardwicke [*vide* Malcolm Smith]).

Specimens of this large species in the collection are as follows: EHT-HMS Nos. 31754-31758 (RE 5169), Phu Phak Khi Nak (mt.), elev. approx. 1300 m., near Ban Nam Yen (subvillage), Kok Sathon (village), Dan Sai (district), Loei (province), "between the ranges of Phu Nam Lang and Phu Lom Lo," Mar. 28, 1955, Robert E. Elbel, collector.

KUMNH Nos. 31380 (RE 556), 31383 (RE 557), Phu Hin Tang (mt.), Latya (district), Kanchanaburi (province), March 25, 1952, Robert E. Elbel; Nos. 31381 (RE 642), 31384 (RE 643), Wang Pho (village), Thong Pha Phum (district), Kanchanaburi (province), Apr. 11, 1952; Robert E. Elbel; Nos. 31385 (Y 11), 31386 (Y 19), 31687 (Y 13), April 3-6, 1952, Phuchik (village), Pak Tho (district), Rat Buri (province), Robert E. Elbel; No. 40106 ♀, Kantalak (dis-

trict), Sisaket (province), May 31, 1954, Robert E. Elbel. No. 40041 "Siam," Dr. Boonsong Lekagul, collector.

One large female (135 mm. snout to vent, tail, 217 mm.) has retained the juvenile coloration. There are two broad continuous lateral stripes; the median stripe is narrower but bifurcates on the neck, and then the two stripes are broken into elongate spots. The venter and area under the tail are uniformly light-colored. The chin and throat are blackish with white flecks except anteriorly.

Physignathus cocincinus Cuvier

Physignathus cocincinus Cuvier, Règne Animal, 2nd ed., vol. 2, 1829, p. 4 (type locality, Cochin China).

One young specimen, EHT-HMS No. 31728 (3821) is in the collection from Phu Phan (mt.), 550 m. (104° 05', 16° 55'), Sakon Nakhon (district and province), Thailand, collected June 29, 1954, by Dr. Boonsong Lekagul and Robert E. Elbel.

This is the largest of the Siamese agamid lizards. In preservation the body and limbs have become plumbeous black. Ten dark brown bands on the lighter ground color of the tail are clearly evident but the terminal part of the tail is uniform brown, lacking bands.

The following characters obtain: snout to vent, 144; tail, 370; femoral pores, 7-6; head length, 42 mm.; width of head, 28 mm.; supralabials, 13-14; infralabials, 10-10.

FAMILY VARANIDAE

This family of large lizards is represented in Thailand by five forms. These are *Varanus rudicollis* (Gray), *Varanus dumerilii* (Schlegel), *Varanus flavescens* Hardwicke and Gray, *Varanus salvator salvator* (Laurenti) and *Varanus bengalensis nebulosus* (Gray). The recent revision of the genus by Robert Mertens (*vide infra*) shows that each of these is a representative of a different subgenus.

Varanus bengalensis nebulosus (Gray)

Monitor nebulosus Gray, in Griffith's Cuvier's Animal Kingdom, vol. 9, Synopsis, p. 27 (type locality, Java).

Varanus nebulosus Smith, Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria. Feb. 7, 1935, pp. 403-404, fig. 94 (4).

V[*aranus*] (*Indovaranus*) *bengalensis nebulosus* Mertens, Abh. Senckenb. Naturf. Ges. Abh., no. 466, 1942, pp. 244-252; pl. 11, fig. 50.

One young specimen, KUMNH 40022 (BL 20002) is in the collection, from Nakhon Si Thammarat, peninsular Thailand, collected

Sept., 1953, by Dr. Boonsong Lekagul. In this the nostril is nearer the eye (5 mm.) than to the tip of the snout (7 mm.); five of the supraoculars are distinctly widened transversely, four of them two to three times as wide as long; a distinct longitudinal groove or depression on the snout; some scales at the tip of snout and in frontal region larger than the other head scales; dorsal body scales, as well as ventrals, smooth or only vaguely keeled.

Chin and throat cream, barred with black; some clouding or spots on side of head and on light supralabial area; body with numerous irregular transverse series of small cream or white ocelli and some indistinct dark transverse bands; the ocellated dots become obsolete on proximal fourth of the tail; two bands of cream on distal fourth, only the more distal one complete. Venter with rows of larger cream dots sometimes more or less connected. The specimen measures: snout-vent, 123 mm.; tail, 150 mm.

FAMILY SCINCIDAE

Mabuya macularia (Blyth)

Euprepes macularius Blyth, Jour. Asiat. Soc. Bengal, vol. 22, 1853, p. 652 (type locality, Rangpur, Bengal).

Mabuya macularia M. Smith, the fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. II, Sauria, 1935, pp. 264-266.

Since there is some doubt about the type locality we propose to fix the type locality at Rangpur, Bengal.

From the variation that obtains in this species it would appear that several subspecific forms will be recognized eventually. The last, most drastic treatment of the species is by Malcolm Smith, *loc. cit.* It has resulted in placing in it, as synonyms, *Euprepes brevis* Günther (type locality, Travancore and Anaimalai Hills); *Mabuya madaraszi* (Méhely * (type locality, Ceylon); *Lygosoma dawsoni* Annandale (type locality, Maddathoray, Travancore) and *Mabuya allapallensis* Schmidt, Allapallai Forest, near Chanda, Central Provinces, India.

However, after synonymizing these Dr. Smith recognizes five forms (numbered from one to five). Four of these are Indian (India, Pakistan and Ceylon) while one is from southeastern Asia and the Malay Peninsula.

In the material at hand from Thailand there are three forms that we are referring to this species. They are distinguished as follows:

* Taylor has revived this name for a Ceylon species. *Ceylon lizards of the family Scincidae*. Univ. Kansas Sci. Bull., vol. 33, pt. 2, Mar. 20, 1950, pp. 481-518, text figs. 1-8; *A review of the lizards of the Ceylon*. Univ. Kansas Sci. Bull., vol. 35, pt. 2, Sept. 10, 1953, pp. 1525-1585.

KEY TO THE THAILAND FORMS OF *MABUYA MACULARIA* BLYTH

1. A postnasal present; no axillary pocket; an area of specialized scales above ankle, providing a chigger-mite "refuge." A somewhat darker lateral band, each scale with a small black spot; scales of the rows below the band each with a similar dark spot, the spots forming rather straight broken lines. A few tiny blackish spots with a cream center scattered on rump . . . *macularia postnasalis*
 No typical postnasal present; an axillary pocket present or absent; a group of specialized scales above ankle providing a chigger-mite "refuge" 2
2. Four dark dorsal lines on back; an axillary pocket; scales on chin and throat with brown borders; scales of the dark blackish lateral band each with a whitish dot; anterior loreal divided leaving a scale behind supranasal (abnormal?) from 1780 m. elevation.
macularia quadrifasciata
 Dorsum olive brown lacking dark lines or spots; no axillary pocket; no distinct white spots on dark lateral stripe, but some darker flecks, spots, or marbling, not forming distinct rows.
macularia malcolmi

The following characters are held in common by these forms: three, five, or seven sharp keels on scales of back and upper parts of sides (all three kinds on same specimen); lower lateral scales smooth or nearly smooth; frontonasal and rostral in contact for a greater or lesser distance; prefrontals separated narrowly, rarely touching at one point; first pair of chinshields separated narrowly or touching at a point; the prefrontals usually touching the second supraocular, occasionally separated from it; supraciliaries normally five, rarely six; seven supralabials four preceding the subocular labial; adpressed limbs overlap, the longest toes reaching palm, wrist, or nearly half-way to elbow.

All forms seen from Thailand have the modified group of scales just above the ankle. The scales are pointed (often partially erect), offering refuge to chigger mites.

There are normally thirty scalerows around the body.

The material available does not suffice to treat of the more western populations of this species. The presence of the "chigger-mite refuges" on the legs seemingly has not been recorded and actually may be absent in western forms.

Mabuya macularia quadrifasciata subsp. nov.

Type: EHT-HMS No. 31802 (RE 5621), Phu Nam Lang (mt.), 1780 m. elev., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand; coll. June 10, 1955 by Robert E. Elbel.

Diagnosis: Four dark dotted dorsal lines on back; scales on chin and throat with brown borders; most scales of sides each with a lighter area; an axillary pocket; anterior loreal usually divided; area of specialized "chigger" scales on leg above ankle.

Description of type: Rostral in contact with frontonasal; supranasals separated; prefrontals separated from each other and from second supraocular; frontonasal touches frontal; no typical true postnasal but first loreal divided transversely leaving a scale behind supranasal; two or three presuboculars; six enlarged palpebral scales on eyelid; frontal longer than its distance from tip of snout, and longer than combined parietals; eight supralabials, five anterior to large subocular (one scale on left side abnormal in size); three primary and three secondary temporals; common frontoparietal suture two thirds of the length of the scales; one pair of nuchals; infralabials seven; mental border on lip much larger than that of rostral; a large azygous postmental; first two pairs of chinshields widened, separated narrowly from each other; five supraciliaries, four supraoculars, two touch frontal; thirty scalerows about middle of body; 15-16 lamellae under fourth toe; a distinct axillary pocket, floored with tiny scales, infested with chigger mites; tail partly regenerated; ear small, rounded, less than half size of a dorsal scale; scales on back quinquecarinate, denticulate behind; on the tail quadricarinate, the two median keels heavier and more widely spaced; scales on leg above ankle especially modified, somewhat pointed, semierect, the area strongly infested with chigger mites.

Color: A dim narrow continuous or dotted dorsolateral light line bordered above by a row of black flecks covering parts of two scalerows; two median scalerows each with a more or less continuous black line, the black extending onto the paravertebral row; laterally a dim broad dark band on side of body and tail bordered below on side of neck by a blue-white dotted line that is more or less continuous with the light line or row of white spots on supralabials; most scales of lateral dark stripe and of rows on side below stripe each with a larger or smaller bluish-white spot or area, producing a polka-dot effect; top of head brown; labial sutures brown or blackish; most scales on chin with brown posterior borders; front part of chin pure white.

Measurements in mm.: Snout to vent, 57; tail, 70 (regenerated); head length, 15; head width, 10; snout to ear, 13; snout to arm insertion, 24; axilla to groin, 25; arm, 17; leg, 25.

Remarks: Most of the dorsal scales are denticulated behind, the number of points depending on the number of keels on the scale.

It would appear that this, like *postnasalis* is a mountain form. The type locality is at an elevation of approximately 5800 ft. The type locality of *postnasalis* is at about 8000 ft. elevation. A specimen of *Mabuya* KUMNH 40114 from Phu Lom Lo (mt.) 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, has been badly injured and most scales are missing from the body. There is an axillary pocket; prefrontals rather widely separated; no postnasal; 14 lamellae under fourth toe; the first chin-shields barely touch mesially. Loss of dorsal scalerows prevents knowledge of the marking on the back but a few scales present on sides show the light spotting. The first loreal on one side is divided. We are unable to offer a satisfactory identification of the specimen. The third form, *macularia malcolmi*, seems to be a lowland form also lacking the postnasal.

Mabuya macularia postnasalis subsp. nov.

Type: KUMNH No. 40110. From Phu Lom Lo (mt.), 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Thailand; collected by Robert E. Elbel, Mar. 30, 1954.

Paratypes: Nos. 40109, 40111, 40112 all with same data.

Diagnosis: A postnasal present; a specialized group of scales on leg above ankle forming a chigger-mite refuge; no axillary "chigger pocket." A dark lateral band present bordered below by a light line; a few scales on rump and those on lower lateral rows with small blackish spots some of which may have a tiny cream spot in center; one or two presuboculars.

Description of type: A small species the limbs overlapping when adpressed; rostral and frontonasal touching; prefrontals narrowly separated from each other and touching the second supraocular; supranasals small, separated; anterior loreal single, higher but narrower than second; a true postnasal present; no scale behind supranasal; one presubocular; usually four enlarged palpebral scales; frontal about equal to its distance to the end of the snout, shorter than combined length of parietals; one pair of nuchals; seven supralabials; three primary and three secondary temporals; frontoparietal suture two thirds of the length of the scales, longer than the interparietal which separates parietals; eight infralabials; mental border on mouth wider than that of rostral; five supraciliaries; four supraoculars, two touching frontal; 30 scalerows around body; 15-16 lamellae under fourth toe; no shallow pocket in axilla; tail complete with 71 subcaudals; ear about half size of a dorsal scale, with some tiny lobules bordering the anterior edge.

Area above foot on hind limb with specialized pointed scales strongly infested with chigger mites; scales of body three or five-keeled, or sometimes seven-keeled, becoming four-keeled on base of tail, the two inner keels stronger and a little wider apart, the median keel absent; scales not or scarcely denticulate behind; scales on sides of neck, on arm and leg, with two or three keels, more distinct on neck and leg. Ventrals smooth and lower lateral scalerows smooth or nearly so.

Two pairs of enlarged chinshields touching labials, the first pair very narrowly separated, the second pair separated by a scale; third chinshields small, separated from labials by an elongate scale; median preanals larger than outer ones; subcaudals slightly wider than adjoining scales.

Color: Above brown or brown olive with a very dim darker lateral band on side, most distinct on neck, bordered above by a slightly lighter line scarcely visible behind neck; there are eight scales on back between darker bands; numerous small dark equal-sized flecks scattered on rump, each with a tiny lighter middle part; along the lateral stripe all scales with a discrete black spot; below this stripe all scales with black dots tending to form rows; one or two similar lines of dots along tail; a distinct light line from tip of snout along supralabials below ear (but including lower edge) and continuing very dimly along side below dark stripe; chin without dark marks; seven median ventral rows of scales uniform, probably white or yellow in life.

Measurements in mm. and scale data on type and paratypes of Mabuya macularia postnasalis, respectively

Numbers	10109	10110	10111	10112
Length, snout to vent	58	55	56	55
Tail	—	80	85	72 broken
Head length	15.5	14	15	—
Head width	10.5	10.2	10.2	—
Snout to ear	12.3	11.2	12	—
Snout to arm	20.5	19.8	18	—
Axilla to groin	29	25.5	24.4	25.2
Arm	19	18.2	17	16.8
Leg	25.5	22.5	23	23
Postnasal	Yes	Yes	Yes	Yes
Prefrontals separated	Yes	Yes	Yes	Yes
Prefrontal touches 2nd supraocular	Yes	Yes	No	Yes
First chinshields separated	Yes	No	Yes	No
Supraciliaries	5	5	5	5
Axillary pocket	No	No	No	No
Chigger "area" on leg	Yes	Yes	Yes	Yes
Scalerows	30	30	30	30

Mabuya macularia malcolmi subsp. nov.

Type: EHT-HMS No. 31774, from Phu Phak Khi Nak (mt.), near Ban Nam Yen (subvillage), Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, Mar. 18, 1955. Robert E. Elbel, coll.

Diagnosis: No trace of an axillary pit, no postnasal, but posterior part of nasal somewhat narrowed; frontal shorter than combined parietal but equal or a little greater than its distance from snout tip, wider than the frontonasal, but touching it; second loreal relatively short, much less than twice as wide as first loreal; a chigger mite refuge on the lower part of leg; leg reaches to elbow when adpressed; first chinshields separated mesially; transverse rows of scales, parietal to above vent, 38; from mental to vent, 47; 30 scale-rows about body.

Color: Above generally olive, each dorsal scale with a slightly darker central area; head darker olive; a dorsolateral stripe on side of head and neck continued on to the anterior part of body, and bordered below by a lighter line from the upper lip; four anal scales whitish.

Mabuya multifasciata multifasciata (Kuhl)

Scincus multifasciatus Kuhl, Beitr. Zool. vergl. Anat., 1820, p. 126 (no type locality stated).

It seems reasonably certain that the specimen described by Kuhl came from the Dutch East Indies, and perhaps most probably from Java. In view of the necessity of fixing a type locality so as to study variation in this widespread species, we propose to fix the locality at Batavia (Djakarta), Java.

The collection contains several specimens of this large form from the following localities:

EHT-HMS No. 31803 (RE 3755), Phu Phan (mt.), Sakon Nakhon (district and province), 550 m. (approx. $104^{\circ} 05'$; $16^{\circ} 55'$), June 20, 1954, Robert E. Elbel and Dr. Boonsong Lekagul. No. 31807 (RE 3947), Phu Kho (mt.), 522 m., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), ($104^{\circ} 22'$; $16^{\circ} 49'$), July 28, 1954, R. E. Elbel and Dr. Boonsong Lekagul. No. 31804 (RE 4485), Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, Jan. 15, 1955, elev. approx. 600 m., R. E. Elbel. 31806 (RE 5245), Ban Bo (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, May 16, 1955, approx. 1780 m., same mountain range as Phu Nam Lang (mt.), but farther north, Robert E. Elbel.

KUMNH No. 40055 (BL 20133) Phatthalung (district and province), Thailand, Nov. 1954, Dr. Boonsong Lekagul, coll. KUMNH No. 40056 (BL 20012) Nakhon Si Thammarat (district and province), peninsular Thailand, Sept. 1953, Dr. Boonsong Lekagul, collector.

KUMNH No. 40113 (RE 3484), Phu Lom Lo (mt.) 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, Mar. 26, 1954, Dr. Boonsong Lekagul and Robert E. Elbel, collectors.

No. 31807 is a gravid female. The dorsolateral line is scarcely discernible in color from the remainder of the dorsum. There are seven dark-brown dorsal stripes on the lateral edges of the dorsal scalerows. The outer scalerow does not extend beyond the shoulder. On the sides there is a brown stripe in which the outer parts of the scales are darker than the median parts. On the area above the arm insertion and posterior to it, the scalerows are directed upwards and backwards. Somewhat farther back on the sides of the body and tail, as well as on the sides of the neck, there are small bluish-white marks heavily bordered by black above and below. The sutures of many of the cephalic scales are edged with black.

One of the males, No. 31804, differs in pattern somewhat. There is a distinct dorsolateral light line bordered above by a light-olive line, the two covering two scalerows and including a row of small triangular dark spots, the second upper row bordered by a distinct black line. The four scalerows separating the black lines display no black except between the shoulders. The head of this specimen is gray-olive.

The keels in this form are normally three. Occasionally the nuchals show four or five keels but sometimes, especially in the very young and females, the nuchals may be smooth. Most specimens and especially females have the keeling reduced on the sides and some specimens have only dim keels on the arm. No. 40055 is striking in having the three keels placed very close together near the middle of the scute leaving the outer third on each side smooth. Thus the space between the series of keels is occupied by wide smooth strips.

The following variable characters obtain: scalerows around middle of body, three with 29, four with 30; transverse rows between parietals and above vent, 41-43; prefrontals touch; the supranasals separated; the prefrontals touch the second supraocular (50 percent); a postnasal invariably present; lobules invariably on front

border of ear-opening; the first loreal lower than second; supralabials, 7-7; the fifth widened, below eye (on one side, in one specimen, eight supralabials with five preceding the subocular labial); four or five large quadrangular scales on the translucent part of the eyelids; supraciliaries, usually 6-6.

The female contains six nearly full-time embryos each still with a bit of the yolk present in the yolk-sack. One embryo measures 35 mm. snout to vent, while the tail is approximately 47 mm. in length. (No. 31806, a recently born specimen in the collection measures 36 mm.) The mother has a snout-vent length of 120 mm. while No. 40056 has a snout-vent length of 125 mm. which is about the maximum size for the species.

Mabuya longicaudata Hallowell

Euprepis longicaudata Hallowell, Amer. Philos. Soc., ser. 2, vol. 11, p. 77, pl. IV, fig. 1 (type locality, "Siam." Here restricted to Bangkok, Thailand). *Eumeces siamensis* Günther, Rept. Brit. India, 1864, p. 91 (type locality, "Siam." Here restricted to Bangkok, Thailand).

Mabuya longicaudata Smith, Fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, Feb. 7, 1935, pp. 270-271 ("The whole of Siam").

KUMNH No. 31397 (RE 520131), Ban Lat (subvillage), Ban Kaeng (village), Phukhio (district), Chaiyaphum (province), Thailand, Jan. 31, 1952. KUMNH No. 31398 (RE 520132), Banpong (city and district), Rat Buri (province), Thailand, Apr. 8, 1952; both collected by Robert E. Elbel.

EHT-HMS No. 31792 (RE 3947), Phu Kho (mt.), 522 m. elev., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, July 28, 1954; collected by Dr. Boonsong Lekagul and Robert E. Elbel.

EHT-HMS No. 23 (BL 1979), Bangkok, Thailand; collected by Dr. Boonsong Lekagul.

Diagnosis: Dorsal scales with two dim or fairly distinct keels, a median (third) keel dimly evident on some scales; supranasals in contact; prefrontals in contact and touching the second supraocular; supralabials seven; 28 scalerows about body; 49 transverse series between parietals and a point above vent; normally the supranasals separate rostral from the frontonasal; subcaudals, 127, 128; leg reaches halfway to elbow of adpressed arm; tail long, often two and one-half times head-body length.

The general color of all is as follows: there is an olive or olive-brown dorsum, and a broad brown stripe from eye to base of tail covering most of three scalerows, bordered above by a dorsolateral

bluish white stripe covering one or one and one-half scalerows. The edges of the dorsal scales are slightly brownish and there appear to be seven dim dorsal brownish lines. On one specimen the dorsolateral light line is invaded by black above and below leaving the line bordered above and below by blackish triangular dots for a part of its length.

All four specimens have 28 scalerows about the middle of the body, and 49 transverse rows between parietals and a point above vent. The lamellae under the fourth toe vary between 24 and 26.

We propose to fix the type locality of this species at Bangkok, Thailand.

Measurements of Mabuya longicaudata

	EHT-HMS	KUMNH	KUMNH	EHT-HMS
Number	23	31397	31398	31792
Snout to vent	92	115	95	—
Tail	227	tip miss.	tip miss.	233
Head length	22	30	21	—
Head width	15	17.5	14	—
Snout to ear	19	24	18	—
Snout to arm	31	36	32	—
Axilla to groin	46	52	48	44
Arm	29	33	30	28
Leg	39	43	39	41

Eumeces quadrilineatus (Blyth)

Plestiodon quadrilineatus Blyth, Jour. Asiat. Soc. Bengal, vol. 22, 1853, p. 652, type locality, China [Hong Kong?]; Taylor, Univ. Kansas Sci. Bull., vol. 23, 1935 (1936, Aug. 15), pp. 452-457.

Eumeces quadrivirgatus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 502 (type locality, Hong Kong).

Diagnosis: Palatine bones not meeting on midline of palate; eyelids scaly; nostril in single nasal; supranasals present; two frontoparietals; pentadactyl limbs; pterygoids toothed; two dorsolateral stripes separated by two scalerows and the edges of two others; three pairs of nuchals.

A specimen of this species, EHT-HMS 31791 (RE 5621) from Phu Nam Lang (mt.), 1780 m. elev., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 10, 1955, Robert E. Elbel, coll., has the following characters: the portion of the rostral visible above equals the greatest length of the internasals. The latter scales are diagonally elongate touching the postnasal behind the nasal, and in contact mesially. The fronto-nasal is about a fourth wider than long, touching the first loreal. The prefrontals are slightly wider than long, forming a common suture. The frontal is a little longer than its distance from the

tip of the snout, as well as longer than the distance from the nuchal. Its posterior border is rounded rather than angular. The frontoparietals are separate, forming a median suture less than a third the length of the scales. The interparietal is nearly a half longer than wide, and is enclosed narrowly by the parietals which are followed by three pairs of nuchals, of nearly equal size.

Three supraoculars border the frontal, the second longer but not quite as wide as third while both are larger than the first. The nostril is pierced in a small nasal. Also, there are present a postnasal, two loreals of which the anterior is higher but only about half the length of the second, seven supraciliaries, two presuboculars, four postsuboculars, eight supralabials of which five are in front of the subocular, and seven infralabials. The mental has a larger labial border than the rostral and is followed by two unpaired postmentals, which in turn are followed by three pairs of chinshields only the first of which is in contact. The last pair of chinshields are followed by an elongate postgenial scale bordering labials, three times as long as wide. The first labial touches the nasal and postnasal. The lower eyelid has an opaque area covered with quadrangular scales larger than those adjoining them. One primary temporal, two large secondary, and two smaller tertiary temporals are present. The ear-opening is small, with three lobules on the anterior border. There are 22 scalerows around the middle of the body. Dorsal scales are large, only two scalerows and the edges of two others lying between the white dorsolateral lines. There are two enlarged preanal scales. The subcaudals, much widened, number 87, the last 16 being on a regenerated part of the tail; 53 dorsal scales from parietals to above the vent. The adpressed limb reaches approximately to the elbow. A greenish or bluish white stripe following the second scalerow passes from the rostral onto tail where it widens and with its fellow practically encompasses the tail posteriorly. A lateral line from the labials passes through the lower part of the ear and continues as far as the groin.

Remarks: The longitudinal scalerows vary from 20 to 22; the transverse rows from parietals to above vent vary between 48 and 54. There are seven or eight supralabials, and the second postmental may be single or divided. The digits of the leg may reach to the base of the fingers or to the elbow of the arm when adpressed.

The amount of known variation in the characters of this species is relatively small, but it may prove to be geographical. One specimen partially digested was taken from the stomach of a *Natrix*

in the collection. The subcaudals are much widened and thus differing from most *Eumeces*. There is only a single divided scale following the vent. The widened subcaudals in the skinks are usually separated from the vent by several rows of small scales.

Dasia olivacea Gray

Dasia olivacea Gray, Ann. Mag. Nat. Hist., vol. 2, 1838, p. 331 (type locality, Penang I. Malaya).

Euprepis olivaceus Günther, The fauna of British India, 1864, p. 80, pl. X, fig. D.

Diagnosis: Dorsal scales finely striate, the striae somewhat sinuous; keels almost obsolete anteriorly; on posterior part of back scales bearing three, five, or seven dim keels; ear-opening greatly reduced, almost covered by large flat scales; second supraocular widely separated from the prefrontal; prefrontals not in contact; 28 scale-rows around body; 43 transverse scale series from parietals to above vent; no postnasal; two anterior temporals. Transverse irregular black bands on body, each scale bearing a bluish-white spot or fleck.

Description of species: Rostral large, its labial border distinctly less than that of rostral, moderately in contact with the frontonasal; latter broader than long (4.9 mm. x 3.7 mm.), and narrowly in contact with the frontal; prefrontals large, separated, touching both loreals; nasals single, much longer than wide, rectangular; supranasals separated, narrower than nasals; six supraciliaries; four supraoculars, three touching frontal; interparietals form a suture for half of their length; interparietal separates the parietals; a pair of nuchals; two presuboculars; two or three postsuboculars; seven supralabials, the fifth below middle of eye, in direct contact with eye granules; four large palpebrals on lower eyelid; two anterior temporals, three secondary and four tertiary temporals; six infralabials; mental followed by a large azygous postmental which is in turn followed by two pairs of chinshields, the first pair in contact; third chinshield small, separated from labials by an elongate scale; frontal longer than combined parietals and longer than its distance from tip of snout. Scalerows, 28 around middle of body; about 44 transverse rows between parietals and a point above vent; about ten preanal scales, the two median enlarged; ear very small, the scales in front large, flat, nearly covering opening; the scales over dorsum and sides of body very finely striate, the striae forming wavy rather than straight lines—from 50 to 100 on each scale; scales of body and sides with low flat-topped keels varying from two to eight on scales in various parts of body, most numerous on scales of the

rump; scales of the posterior part of forearm usually dimly tricarinate, the fine striae continued on scales to the tips of the digits.

When limbs are adpressed the digits overlap; palm covered with rounded moundlike scales; the lamellae broad, not keeled; no enlarged scale at wrist; scales on sole similar to those of palm but a pair of enlarged scales at heel; subdigital lamellae broad, unkeeled, 19 under longest toe; tail broken, the subcaudals widened; scales on venter smooth.

Color: Body brownish gray with a series of dark irregular transverse bars across the neck and body each scale of which has a silvery or bluish-white fleck or spot; head with small somewhat symmetrical marks, pronounced in occipital region and on the supracoculars; limbs with some darker flecks suggesting bands.

Measurements in mm.: Snout to vent, 100; tail broken and partly lost; head width, 14.5; head length, 24.2; snout to ear, 20; snout to foreleg, 33; axilla to groin, 50; arm, 28; leg, 36.

Remarks: The specimen described is KUMNH No. 40057 from Nakhon Si Thammarat, peninsular Thailand, south of the Isthmus of Kra. While the type locality is relatively near (about 200 mi. south and on a coastal island) there are certain differences. The ear differs in its general make-up and appearance; the frontonasal is longer than broad. We have found no mention in the literature of the curious striation of the scales of this species. It is possible that it has been overlooked, yet it is also possible that it differs from the typical species of *Dasia* in this character.

It may be noted that *Mabuya longicaudata* has developed extensive striation on scales while most species of *Mabuya* lack the striae altogether.

Sphenomorphus indicus indicus (Gray)

(Fig. 16)

Hinulia indicum Gray, Ann. Mag. Nat. Hist., ser. 2, vol. 12, 1853, p. 388 (type locality, "Himalayas." The type locality is restricted to "Sikkim, Himalayas" by Stejneger, *loc. cit.*).

Sphenomorphus indicus Stejneger, U. S. Nat. Mus. Bull. 58, 1907, pp. 216-218, pl. 17, fig. 1 (from Boulenger).

Lygosoma indicum Boulenger, A vertebrate fauna of the Malay Peninsula from The Isthmus of Kra to Singapore . . . Reptilia and Batrachia, 1912, p. 87, fig. 24; Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, June, 1916, p. 55 ("Hills near Pre [northern Siam]"); Bull. Raffles Mus., no. 3, April, 1930, pp. 33-34.

This species unfortunately had no type locality given except "Himalayas." The generalized locality "Himalayas" has been fixed by Stejneger (*loc. cit.*) to Sikkim, Himalayas, which should suffice



FIG. 16. *Sphenomorphus indicus indicus* (Gray).
KUMNH No. 40108, Phu Lom Lo (mt.), 2100 m.,
Kok Sathon, Dan Sai, Loei (province), Thailand.
Actual total length, 199 mm.

since the species occurs in this rather small Indian State, lying in between the countries of Nepal and Bhutan. From here the species ranges across southern China to Formosa, and south through Burma, Assam, Thailand, Indo-China and parts of Malaya. Knowledge as to whether or not it has developed subspecific forms in this vast range other than now recognized must await a review of considerable material. It is not a common species and seemingly it is not evenly distributed in Thailand. It is believed that *S. i. zebratus* Boulenger (1887) from Tenasserim should be recognized as a subspecies.

Two specimens of *S. i. indicus* are in the collection (KUMNH No. 40107-40108 (RE 3536-3567) from 2100 m. elev., on Phu Lom Lo (mt.), Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, March 30, 1954, Dr. Boonsong Lekagul and Robert E. Elbel, collectors.

Diagnosis: No supranasal; frontonasal touches rostral; divided frontoparietals; prefrontals touch; nostril in a single nasal, no postnasal; lower eyelid scaly; parietals enclose interparietals; only four supraoculars; a dark lateral band from eye to groin, indefinite on lower side.

Description: (KUMNH No. 40107): Rostral convex, not flattened, forming a broad suture with the frontonasal which is much broader than long; prefrontals separated; the frontal shorter than the combined parietals, nearly a half longer than its distance from tip of snout; parietals enclose interparietal; a pair of nuchals separated from secondary temporals by a pair of tertiary temporal scales; four supraoculars, last touching large upper secondary temporal; eight or nine supraciliaries; two loreals, second widest, slightly lower than first; no postnasal; two preoculars, lower large; nine scales form a pre-, sub- and postocular series extending to the temporal; two or three small scales between last supraocular and the postoculars (sometimes described as small supraoculars); supralabials seven, the fifth and sixth below eye; infralabials seven; a pair of superimposed anterior temporals; a pair of larger secondary temporals, the upper touching the parietal, three tertiary, the upper lying behind parietals; a pair of large preanals.

Mental wider than rostral; postmental single, followed by two large chinshields in contact and these by a second pair separated by one scale, a third pair following separated by five scales; the chinshields all in contact with the labials; ear-opening moderate (1.6 mm. x 2 mm.), granules but no lobules on anterior border; lower

eyelid scaly without transparent disc; scalerows around body, 36; transverse scale series from parietals to above vent, 78; lamellae under fourth toe, 19-20 (95 subcaudals in No. 40108).

Color: Above olive-gray on head and dorsum; a dark lateral band from eye, passing above ear-opening then widening and continuing to groin, the upper edge well defined and bordered by a dim light line, its lower edge ill defined, generally covering much of three scalerows. All ventral surfaces immaculate except for some dim gray areas under sides of neck. A few dark flecks on dorsal part of neck, shoulder region, and a few near base of tail. Tail reproduced.

Measurements in mm. (of KUMNH Nos. 40107, 40108, respectively): Snout to vent, 95, 79; tail, —, 120; snout to ear, 17.5, 14.5; head length, 20, 18; head width, 15, 12.5; snout to arm insertion, 30, 26; axilla to groin, 53, 43; arm, 22, 20; leg, 33, 32.

Remarks: The second specimen agrees with the one described in most characters, but the supralabials have more or less distinct black spots on the sutures. The tail has a narrow dorsolateral black line to tip, and the olive back has more numerous but smaller dark flecks. On the median dorsal line of the tail there is a row of black dots. Toward the end of the tail most of the scales have blackish dots.

The hind limb in the young and in males reaches to the elbow; in large adult females they barely overlap. Both specimens have nuchal scales separated from the large secondary temporals by an enlarged tertiary temporal scale.

Boulenger states "nostril in a nasal or between nasal and post-nasal." We would suspect that the latter condition betokens a different form from *indicus*. There is not a trace of "large spots in flanks" mentioned by Boulenger (Cat. vol. 3, pp. 241-242, 1887).

Sphenomorphus maculatus (Blyth)

(Fig. 17)

Lissonota macula'a Blyth, Journ. Asiat. Soc. Bengal, vol. 22, 1853, p. 653, (type locality, Assam).

A specimen of an adult gravid female lizard (EHT-HMS No. 31781 [RE 3887]) has the following characters that ally it with *maculatus*:

The rostral has a distinct concavity just in front of its straight transverse suture with the frontonasal. The prefrontals are widely separated. Of the five supraoculars, three touch the frontal. There are 34 scalerows around the middle of the body. While there are no distinct nuchals the median scales on the neck are usually widened.

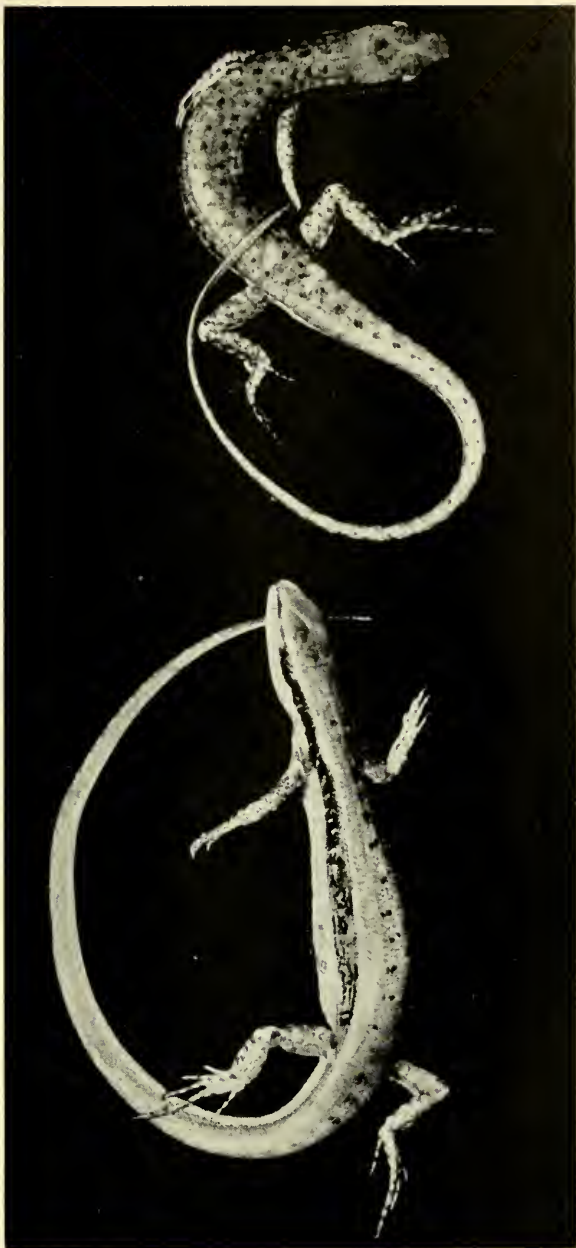


FIG. 17. *Sphenomorphus maculatus* (Blyth). Upper figure, EHT-HMS No. 31784, actual total length, 161 mm. Lower figure, EHT-HMS No. 31781, actual total length, 176 mm. Both from Phu Kho (mt.), 522 m. elev., Kan Luang, Na Kae, Nakhon Phanom (province), Thailand.

A stripe from the rostral passes through the eye, then widens and continues along the side. It is black anteriorly with a few small white spots, then more olive posteriorly, tending to form four narrow dark lines and three olive lines. The stripe continues along the side of the tail to tip but there it is nearly a uniform olive, edged with a scalloped brown line. A discreet white stripe from behind eye passes above the ear to the hind leg where it is interrupted, but continues somewhat indistinct for some distance on the tail. Below this the labials and sides of neck have some small dark spots or flecks, while below the lateral white line there is an indefinite darker stripe, broken anteriorly. The chin, venter, underside of limbs, and the subcaudal area are immaculate whitish-flesh. The dorsum is olive with dim paired dark dots on either side of the median line, and its outer border has a more or less distinct very narrow lighter line.

In a young specimen from the same locality and lot, the median paired dark spots are somewhat indistinct but the dorsal olive color is separated from the deep black lateral stripe by a narrow indefinite light line. A lateral white line is present, the edges irregular but clearly defined. Below this white line the black is arranged in a row of 18 spots, and the series is more or less continuous in front of thigh and tibia.

The two males (Nos. 31783-31784) lack the distinctive white lateral stripe. Their legs are longer and they show some other small differences in the color pattern. Seemingly the subcaudal count is lower and scalerows around the middle of the body higher (38).

The leg reaches to the elbow on the female distended with eggs. In males the leg reaches the axilla or a little beyond.

The specimens are from the following localities: EHT-HMS No. 31780 (RE 3755), Phu Phan (mt.), 550 m., Sakon Nakhon (province and district), Thailand, (104° 05', 16° 55'), June 20, 1954, R. E. Elbel and Dr. Boonsong Lekagul, colls. 31781-31784 (RE 3887), Phu Kho (mt.), 522 m., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, (104° 22', 16° 49'), July 19, 1954, Dr. Boonsong Lekagul and R. E. Elbel, colls.

Measurements in mm. and scale data for Sphenomorphus maculatus

Number and sex	Snout-vent length	Tail length	Total length	Dorsals to vent	Sub-caudals	Scalerows middle	White lateral line
31781 ♀ ...	64	112	176	79	132	34	yes
31783 ♂ ...	57	111	168	77	124	38	no
31784 ♂ ...	59	102	161	75	123	38	no
31782 ? ...	28	—	—	80	—	38	yes
31780 ♀ ...	60	—	—	80	—	36	yes

Genus *LEIOLOPISMA* Fitzinger

The species of *Leiopisma* * may be recognized by the following characters: rostral and frontonasal in contact; parietals enclose interparietal; four large supraoculars; six or seven supralabials; no supranasals; lower eyelid with an undivided transparent disc; limbs pentadactyl; prefrontals touch (in Thailand forms) usually making a substantial suture.

The following species are represented in the collection: *Leiopisma eunice* Boulenger, *L. rupicola* Smith, *L. siamensis* sp. nov. Besides these the following occur:

Leiopisma kohtaoensis Cochran (spots on throat; 30-32 scalerows; one or more nuchals; 16 lamellae under toes; limbs of adults not touching when adpressed). An island form which may or may not occur in peninsular Thailand (see Malcolm Smith, Fauna Brit. India, Rept. Amph. vol. 2, p. 297).

Leiopisma v. vittigerum Boulenger [= ? *Leiopisma pranensis* Cochran] (with a median white or golden stripe from snout to tail, usually bordered with black; in juveniles often three light stripes present on body; 28-30 scalerows).

Leiopisma doriae Boulenger (three or four pairs of nuchals; 28-32 scalerows; six scalerows across back; dorsals much larger than laterals; prefrontals barely touching).

? *Leiopisma melanostictum* Boulenger (34-38 scalerows; back dotted with black; a broken lateral stripe present).

Leiopisma tavesae Smith (26 scalerows; longitudinal streaks on back and neck).

Leiopisma r. reevesi Gray (eight scalerows above on back; 28 scalerows around body; several pairs of nuchals present).

Leiopisma rupicola (M. Smith)

(Fig. 18)

Lygosoma rupicola M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 46 (type locality, "Chong Kae, near Paknam, central Siam").

Two specimens, EHT-HMS Nos. 31786-31787 (RE 3887) are in the collection from Phu Kho (mt.) 522 m. elev., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, July 19, 1954, Dr. Boonsong Lekagul and Robert E. Elbel, collectors. These specimens have the following characters:

* Malcolm Smith, in a paper published in Records of the Indian Museum, vol. 39, pt. 3, Sept. 1937, pp. 213-234 (p. 223), treats of *Leiopisma* as a section under the genus *Lygosoma* (if we interpret his arrangement correctly). He states, "Under *Leiopisma* are included a number of species that cannot clearly be assigned to any genus . . . The majority of the *Leiopismids* have no doubt been derived from *Lygosoma* by the simple change in the eyelid, others from *Emoia* by loss of the supranasal shield through fusion with the nasal."

The general markings are shown in the figure. The color is variable light brown on dorsum and sides growing much lighter towards the venter. The spots are black, the lateral stripe broken by white or yellow spots. The venter is yellowish or whitish. The number



FIG. 18. *Leiolopisma rupicola* (M. Smith). Left figure, EHT-HMS No. 31787, actual total length, 45 mm.; right figure, EHT-HMS 31786, actual total length, 87 mm. Both specimens from Phu Kho (mt.), 522 m. elev., Kan Luang, Na Kae (district), Nakhon Phanom (province), Thailand.

of scalerows around the middle of the body is 34, the lamellae under fourth toe 18 or 19. There are 117 subcaudals in No. 31786, the median series slightly enlarged. Under a lens, scales indefinitely roughened on surface by from ten to twenty fine irregular longi-

tudinal lines covering all but front edge of the scale; venter scales smooth while the greater part of the tail is likewise smooth.

The snout-vent length of No. 31786 is 32 mm., the total length 87 mm.; of No. 31787, 29 mm.; tail lost. The leg reaches the elbow of the adpressed arm or a little farther.

Leiolopisma eunice Cochran

(Fig. 19)

Leiolopisma eunice Cochran, Proc. Biol. Soc. Washington, vol. 40, Dec. 2, 1927, pp. 187-188 (type locality, Bang Suk near Pak Jong,* Thailand), USNM No. 72180 (Dr. Hugh Smith, coll.); Proc. U. S. Nat. Mus., vol. 77, 1930, p. 18, fig. 3 (Doi Angka, 700 ft., and Pak Jong*).

Leiolopisma reevesi reevesi Smith, The fauna of British India including Ceylon and Burma; Reptilia and Amphibia, vol. 2, Sauria, 1935, pp. 295-296.

Diagnosis: A small form reaching 56 mm. snout to vent; anterior loreal much higher and narrower than second; eight supralabials,



FIG. 19. *Leiolopisma eunice* Cochran. EHT-HMS No. 31785, Ban Muang Khai, Tha Li (village), Tha Li (district), Loei (province), Thailand. Actual snout-to-vent length, 43 mm.

the sixth and seventh largest, below eye; one large anterior temporal; three secondary and three tertiary temporals; one distinct pair of nuchals; ear three or four times size of the palpebral disc; 32 scalerows around middle of body; two much enlarged anals flanked by two smaller scales; toes of adpressed limbs overlap two to three millimeters; four supraoculars.

A specimen (EHT-HMS No. 31785 [RE 4390]) from Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, elevation approx. 600 m., Dec. 29, 1954, R. E. Elbel, coll., has the following characters: rostral convex reaching back to

* Pak Jong = Pakchong, Doi Pia Fai Mts.

a line connecting the front edge of nostrils, broadly in contact with the frontonasal, which is much wider than long; prefrontals broadly in contact, each nearly as large as the frontonasal; frontal slightly longer than its distance from the tip of snout, more than a third shorter than the combined parietals; frontoparietals paired, each larger than the interparietal; latter enclosed by parietals; temporal formula, $1 + 3 + 4$; supralabials eight, five preceding first subocular labial; a row of small suboculars below eye, the series broken medially so the first subocular labial is in contact with small granules of eyelid; a transparent eye-disc one third or one fourth of the area of ear-opening; labial borders of mental and rostral nearly equal; infralabials six, the last nearly concealed by last supralabial, first small; a large undivided postmental; three pairs of chinshields, the first in contact, second separated by a scale, third pair by three scales, fourth pair small separated by seven scales; all four of the chinshields touching labials. Most of the tail missing. Transverse scale series from parietals to above vent, 70; the distance between snout-tip and arm-insertion (15.4 mm.) is contained in the axilla-to-groin distance (20.2 mm.) 1.31 times. There are 17 lamellae under the fourth toe; eight scalerows between dorsolateral lines.

The color above gray-brown with very numerous fine black flecks, the larger flecks tending to be more numerous towards the middle line of the back; the dorsolateral black line, bordered by a dim line of very light tan, is more or less broken up by cream vertical bars into about twenty spots; on neck the line is nearly solid black posteriorly but it narrows and becomes broken behind eye; a black line across edges of eyelids, and a dark line across loreal region to rostral; arm and leg marbled or reticulated above; sides with a few fine scattered flecks; sutures of labials with indefinite dark spots.

Remarks: Dr. Cochran has suggested that *Leiolopisma eunice* has several pairs of nuchals. In the several species the scales on the neck are widened in the four dorsal rows. This is true in the described specimen but only the first pair are modified enough to be considered nuchals. Dr. Cochran's statement is "several pairs of feebly enlarged nuchals." The presence of 34 scalerows would, in my opinion, preclude association with the *Leiolopisma reevesi* from Ningpo. Malcolm Smith, however, has referred *L. eunice* to the synonymy of *L. reevesi reevesi* as a subspecies.

Leiolopisma siamensis sp. nov.

(Fig. 20)

Type: EHT-HMS No. 31788 (RE 3936) from Phu Kho (mt.), 522 m., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, ($104^{\circ} 22'$; $16^{\circ} 49'$), collected by Dr. Boonsong Lekagul and Robert E. Elbel, July 26, 1954.

Diagnosis: Prefrontals meet at a point; nostril in a nasal; no supranasals; large undivided disc on lower eyelid, less than one third of



FIG. 20. *Leiolopisma siamensis* sp. nov. EHT-HMS No. 31788, Kho Mt., 522 m., Kan Luang, Na Kae (district), Nakhon Phanom (province), Thailand. Actual total length, 116 mm.

the size of the ear; tympanum deeply sunk, three lobules barely indicated on border; sixth labial separated from large upper temporal by two temporal scales; fifth labial separated from it by one temporal scale; snout to arm insertion 19.5 mm.; axilla to groin, 24 mm.; 34 scalerows about middle of body; hind leg reaches elbow of arm; 20 lamellae under fourth toe; subcaudals not or but slightly widened except on regenerated part, lateral body scales as large as dorsals; a double frontoparietal; enlarged preanals; small median pair of nuchals, flanked by a larger one laterally; ear-opening 1.5

mm. x 1.1 mm. No black markings of any sort; brown above, growing light low on sides; venter, chin, throat, subcaudal region, and lower part of sides immaculate, without trace of pigment.

Description of species: Rostral large, length of the part visible on top of snout minutely less than its distance from frontal, broadly in contact with frontonasal; latter twice as wide as long, touching anterior loreal and nasal laterally; prefrontals meeting mesially at a point as do the frontal and frontonasal; frontal a third longer than its distance from tip of snout, shorter than interparietal and frontoparietals together; parietals broadly in contact behind interparietal; nostril in a single nasal, without a postnasal; two loreals, the anterior narrower and higher than second; two unequal superimposed preoculars; four large supraoculars, two touching frontal; 8-9 supraciliaries, first largest; an undivided transparent disc in lower eyelid; seven supralabials, the fifth and sixth largest below eye but separated from orbit by two irregular rows of suboculars; a wedge-shaped scale inserted partially between the fourth and fifth supralabials; two anterior temporals followed by two secondary, the upper very large; tertiary temporals four, the upper lying behind the parietal, separated from its fellow by a pair of nuchals; anterior temporals separated from eye and last supraocular by two or three rows of postoculars; tympanum deeply sunk; ear-opening large, rounded, oval, about size of eye-opening, three or four times size of the disc in the eyelid; about 65 scales from parietals to above vent; 34 scalerows about middle of body; subcaudals not or but slightly wider than adjoining scales except where tail is regenerated in which part the subcaudals are greatly widened.

Color: Generally light brown above with a faint indication of a lighter line on dorsolateral nuchal area separated from its fellow by six scalerows and disappearing back of shoulder; indication of a faint darker line from behind eye, passing above tympanum and above arm below dorsolateral line; faint indications of darker areas continue some distance on sides. Venter and all undersurfaces immaculate whitish lacking any trace of pigment except on hand and foot. Top of head a little darker than body.

Measurements in mm.: Snout to vent, 51; tail (regen.), 65; snout to arm insertion, 19; axilla to grain, 24.5; length of head, 13; width of head, 7.3; length of arm, 14; leg, 20.

Remarks: This species belongs in that group of the genus having the lateral and dorsal scales subequal, and a very large ear-opening which approaches the open eye in size. It differs from

L. reevesi in having the limbs overlap a greater distance (to elbow); more scalerows around body, no black marks on body; a pair of nuchals flanked by an enlarged outer pair of tertiary temporal scales, and three anterior temporals, instead of two.

From *melanostictum* it differs in having a greater overlap in the adpressed limbs, much enlarged preanals, the absence of distinct black markings on body, and in the distance from snout to arm insertion. The distance from axilla to groin is slightly less proportionally.

Leiopisma eunice Cochran, a species described from Bang Suk near Pakchong, Siam, differs in having a short snout, the limbs when adpressed failing to meet and the distance between axilla and groin is double that from tip of snout to arm insertion.

SUBORDER SERPENTES

FAMILY TYPHLOPIDAE *

Typhlops diardi mülleri Schlegel

Typhlops mülleri Schlegel, *Abbildungen amphibiens*, 1839, p. 39, pl. 32, figs. 25-28 (type locality, Padang, Sumatra).

Typhlops diardi Schlegel, *Abbildungen amphibiens*, 1839, p. 39 (type locality, Indes Orientales); Smith, *The Fauna of British India, Ceylon, Burma*.

. . . *Reptilia and Amphibia*, vol. 3, *Serpentes*, 1943, pp. 51-52, fig. 15 (synonymy and literature).

Typhlops schneideri Jan, *Iconographie générale des ofidiens*, tome 1, livr. 9, 1864, p. 20, pl. I, fig. 3, (type locality, Bangkok, Siam).

Typhlops siamensis Günther, *Reptiles of British India*, 1864, p. 175, pl. 16, fig. D (3 figs.) (type locality, Siam).

Typhlops diardi mülleri Brongersma, *Zool. Meded.*, Leiden, vol. 17, 1934, p. 193.

The single specimen of *Typhlops diardi mülleri* in the collection is KUMNH No. 31436, from Chantuk (village), Sidiu (district), Khorat (province), Thailand; Robert E. Elbel, coll., Aug. 31, 1952. It agrees with the subspecies *mülleri* as to the color markings. There are 26 scalerows around the body near the middle, the eleven dorsal scalerows being dark brown, the remaining fifteen rows cream-white in color. Farther forward the white color impinges on the adjoining row until only nine dorsal rows are dark brown, and seventeen are cream-white. There are 305 transverse scalerows from the mental to the vent, and eight rows on the tail, counting the terminal spine. The total length is 332 mm., the tail 4.5 mm.

The nasals are incompletely divided. They form a very narrow contact behind the rostral (which is not mentioned as a character

* We do not follow the recently proposed idea that the Typhlopidae are not serpents. It is not improbable that the Serpents are diphyletic in origin.

in either of the subspecies). The eye is distinct and lies wholly below the surface of the ocular scale. All anterior head scales have minute tubercles. The anterior nasal scale covers a depression below the nostril.

Held in certain lights the scales show a most elaborate criss-crossing striation on the undersurface of their exposed free parts. This is more evident when the scale is removed and viewed from below. This condition has also been observed in other species of *Typhlops*.

FAMILY DIPSADIDAE

Pareas macularius Theobald

(Fig. 21)

Pareas macularius Theobald, Jour. Linn. Soc., vol. 10, 1868, p. 54 (type locality, Martaban, South Burma).

The single specimen of *Pareas macularius* in the collection is EHT-HMS No. 31798 ♀. It is definitely from Thailand but the exact locality is uncertain owing to the disintegration of the tag.

Diagnosis: This species, which resembles *Pareas margaritophorus* Jan somewhat in color and markings, differs from it, however, in having a more compressed body, keels on the seven median scale-rows, and a somewhat larger series of ventrals and subcaudals. It seems to replace *P. margaritophorus* in Burma, Bengal, northern Thailand and Indo-China. The following characters are evident in the specimen at hand:

Description: Rostral large, slightly wider than high, its upper edge a straight transverse line; internasals more than twice as wide as long, notching upper line of the nasal, narrower than prefrontals; latter wider than long, touching preocular and loreal, entering orbit; frontal short, six-sided, its length greater than its width, longer than its distance from tip of snout, shorter than parietals; latter scales longer than their distance from tip of snout; nostril in a single nasal somewhat triangular; loreal about as wide as high; one preocular, one postocular; a large narrow curving subocular; supraocular not longer than eye; temporals two and three, however, they are irregular in second and third rows; seven supralabials, none entering eye, four or three touching subocular, last much the largest; mental small, touching one of the first pair of chinshields; eight (seven) infralabials, four (or five) touch first chinshields; second and third pairs of chinshields transverse, followed by first ventral, which is larger than succeeding scales. Eye distinctly larger than its distance to mouth.

Scales on back of head 20; 15 scalerows on neck, middle of body, and in front of vent. Ventrals 163, subcaudals 55, paired; anal single. Total length, 210 mm. Tail, 49 mm. Mandibular teeth, 29, the anterior 5 times as large as the posterior.

Color: The top of the head heavily speckled with brown; a pair of black-brown spots behind parietals; a diagonal brown line from upper level of eye to mouth angle; on seventh labial a suggestion



FIG. 21. *Parcas macularius* Theobald. EHT-HMS No. 31798 ♀, "Thailand." Actual total length, 210 mm.

of a second line from lower part of eye across the suture of the sixth and seventh labials; brown flecking on labials; a light nuchal band from which a process runs forward behind eye, and joins the light color of chin and throat behind jaw angle. General body color brown with approximately 60 transverse rows of small black dots or spots, each bordered in front by white on the same scale, the rows irregular and often incomplete. Outer part of ventrals and

subcaudals flecked with brown. A deep black W-shaped mark on neck preceded by an irregular neckband, yellowish (in life).

A photograph is shown.

Pareas carinatus Boie

(Fig. 22)

Pareas carinatus Boie, Isis, 1828, p. 1035 (type locality, Java).

The two specimens of *Pareas carinatus* are, EHT-HMS No. 31796 (RE 5246) Ban Po (subvillage) approx. 1780 m. elev. ("in the same range as Phu Nam Lang (mt.) but farther north"), Na Haeo (village), Dan Sai (district), Loei (province), Thailand, May 16, 1955, and EHT-HMS No. 31797 (RE 5610), Phu Nam Lang (mt.), 1780 m. elev., Ban Khok (subvillage), Na Phung (village), Kan Sai (district), Loei (province), Thailand, June 10, 1954, both collected by Robert E. Elbel.

No. 31797 ♀. The body is strongly compressed. The rostral of this species is much narrowed and visible above only as a point. The internasals, longest mesially, are one and a half times as wide as long. The prefrontals bend down on the sides of the head but do not enter orbit, the suture between them being a little longer than the internasal suture. The frontal is six-sided, the sides subparallel, longer than its distance to the tip of the snout and equally as large as the parietals. The supraocular is longer than the eye. The nasal is as high as long, the loreal distinctly higher than wide. The first pair of infralabials touch behind the mental. The first pair of chinshields is not longer than the second or third transverse pairs.

The color is nearly uniform brown, finely peppered with darker pigment. The venter is whitish with a row of irregular dark flecks on outer edge of ventrals and a discontinuous row of flecks in the middle of venter. A narrow line runs from eye back to the scalerow bordering the median row, and is lost almost immediately. The chin and neck are white, the head peppered with black flecks. Some trace of the dorsal markings, obvious in the male, may be discerned if the specimen is submerged in clear liquid.

No. 31796 ♂ displays some 78 narrow dark slightly diagonal transverse markings, each having a width of less than a single scale, extending laterally to the ventrals. There are 7-7 supralabials, and 8-9 infralabials. Otherwise it agrees generally with the female in squamation. There are 77 dim dark bands on body formed by scales having a little black pigment on their edges. The median scalerow is nearly uniformly colored in dark gray with the centers of the scales a little lighter because of less gray pigment. The eye

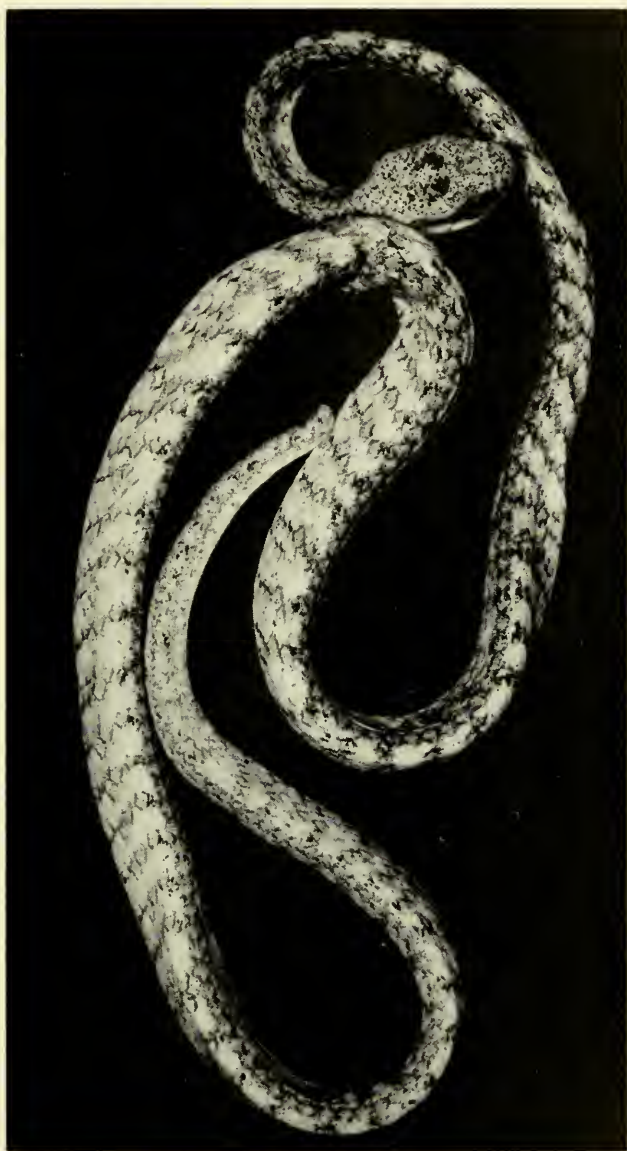


FIG. 22. *Pareas carinatus* Boie. EHT-HMS No. 31796 ♂, Ban Bo, Na Haeo, Dan Sai, Loei (province), Thailand. Actual total length, 430 mm.

is one-half times greater in diameter than its distance from the mouth, and equals the length of the snout in front of the eye. The head markings differ from the female in having a threadlike line running below the eye to the seventh supralabial. Three series of ventral spots or flecks are present. The median scalerow in the posterior part of the body is somewhat enlarged. The pupil is vertical.

There are 5 subequal maxillary, and 23 mandibular teeth, the anterior ones two to three times the size of the posterior. The distal half of the maxillary teeth have some distinct striations.

Data on Pareas carinatus Boie

Number	Scale-rows	Ventrals	Sub-caudals	Supra-labials	Infra-labials	Maxillary teeth	Mandibular teeth	Total length
31796	19, 15, 15, 15	181	26 +	7-7	8-9	5-5	23	430
31797	21, 15, 15, 15	178	71	6-7	8-5	5-4	23-21	522

In both there are 1-1 preoculars, 1-1 postoculars, 3-3 suboculars. The temporals are 3 + 4 + 3, and 3 + 3 + 4, respectively.

FAMILY COLUBRIDÆ

SUBFAMILY SIBYNOPHINÆ

Sibynophis collaris triangularis subsp. nov.

(Fig. 23)

Type: KUMNH No. 33520 (RE 233), Nongko (village), Siracha (district), Chon Buri (province), Thailand, Dr. Boonsong Lekagul, collector, Aug. 18, 1953.

Diagnosis: Related to *Sibynophis collaris* but differs in having the black nuchal band reduced to a triangle bordered on two sides by cream lines two scales wide, which are continuous with the cream line on labials; a series of cream or yellow spots chiefly on the fourth scalerow.

Description of subspecies: Rostral three-fifths times as high as wide, narrowly visible above; internasals a little wider than long, their posterior borders curving, laterally narrowed, touching loreal; frontal a little wider than supraocular (4 mm. x 2.5 mm.), longer than its distance from end of snout; parietals longer than wide, about equal to distance from rostral; nasal scale at least partially divided with a vertical depression following nostril, the posterior portion higher than anterior, touching two supralabials; loreal small, longer than high, touching two supralabials; a large preocular higher than wide; ten supralabials, the fourth, fifth and sixth enter orbit, the sixth and seventh touch lower postocular but the single anterior

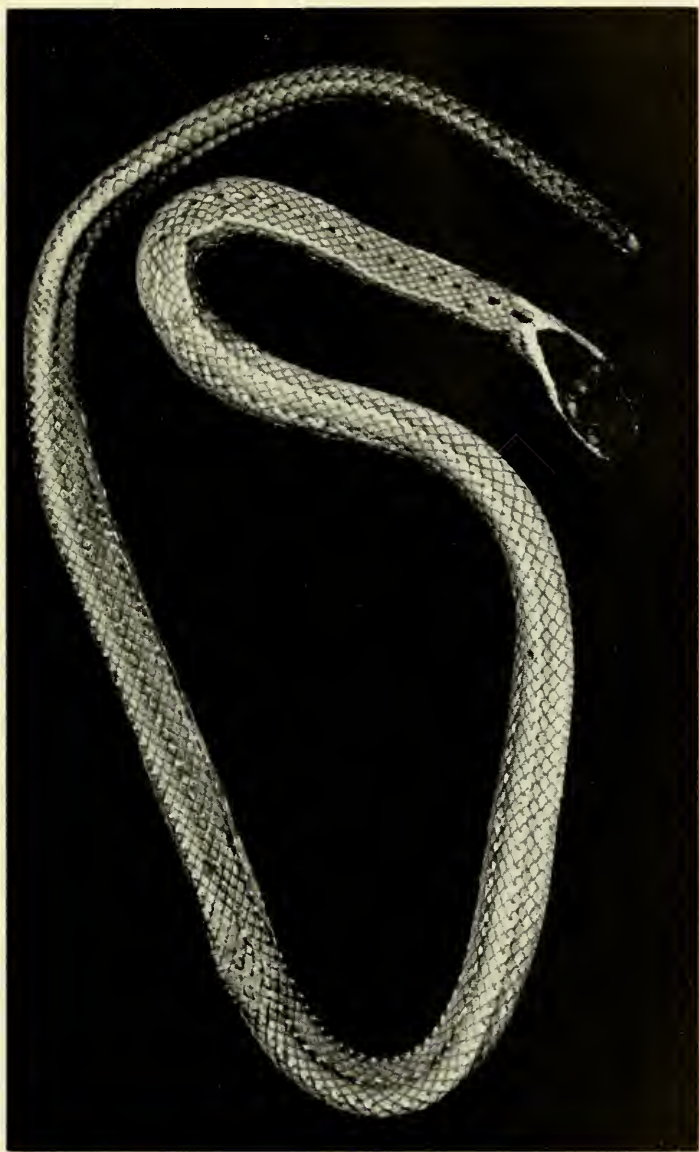


FIG. 23. *Sibynophis collaris triangularis* subsp. nov. Type. KUMNH No. 33520, Nongko (village), Siracha (district), Chon Buri (province), Thailand. Actual total length, 327 mm.

temporal touches only the eighth; tenth and last supra'labial much the largest of the series; two postoculars; the parietal touching only the upper postocular which is nearly square; the temporal formula is $1 + \frac{1}{1+1}$; nine infralabials, the fourth largest, the first four touching the first chinshields which are larger than second pair; scales smooth; scalerows, 17, 17, 17; ventrals, 160; anal divided; subcaudals (incomplete), 49.

Color: Generally grayish brown with a fawn line beginning on neck at level of the eleventh ventral, following the fourth and part of fifth scalerows; somewhat farther back it becomes discontinuous forming elongate or rounded spots on the upper half of the fourth scalerow, sometimes including a part of the adjoining scale in the fifth row; pigment surrounding these spots becoming somewhat blackish; on the middorsal line a row of black spots continues for a short distance; farther back a discontinuous series of white dots begins and continues posteriorly; these finally become obsolete but they can be traced onto the tail; ventral surface whitish with a discreet rounded black spot on each ventral and subcaudal; the outer turned-up part of the ventrals pigmented like the lateral body scales.

Head variegated olive with brownish-black spots, one or two on each head scale; an indefinite transverse band across back of frontal and supraoculars. A second somewhat curving indefinite band bordering parietals and temporals, joining the deep black triangular nuchal spot and thus enclosing an olive area; a cream line from rostral passes back across the labials and meets its fellow on the median nuchal region; this bordered above on labials with black; on the lower part of some labials black spots present; the anterior part of infralabials light brown with darker-edged cream spotting.

Dentition: Maxillary teeth, 49-47; mandibular teeth, 53-52; palatine-pterygoid series, 53-53.

Measurements in mm.: Snout to vent, 239; tail (mutilated), 88; head width, 8.15; head length, 14.

Remarks: The snakes of this group (Sibynophinae) show a large percentage of individuals with mutilated tails. The senior author has recently pointed out that at least one species of the genus *Scaphiodontophis* also a member of the Sibynophinae, is capable of casting off the tail to escape. This is a habit common in lizards. Autotomy possibly is a subfamily character and may account for the mutilation so common in species of both genera of the subfamily. Possibly it is a primitive character of serpents harking back to some Saurian ancestor. The senior author has found a certain popula-

tion of gartersnakes (*Thamnophis*) with mutilated tails but in that particular case it was obviously brought about by disease. No such diseased condition has been reported in any sibynophid snake.

Malcolm Smith has observed this form, and in his *Serpentes*, vol. 3 of the "Fauna of British India" calls attention to it as follows: "Specimens from Siam and Annam may have a lateral series of

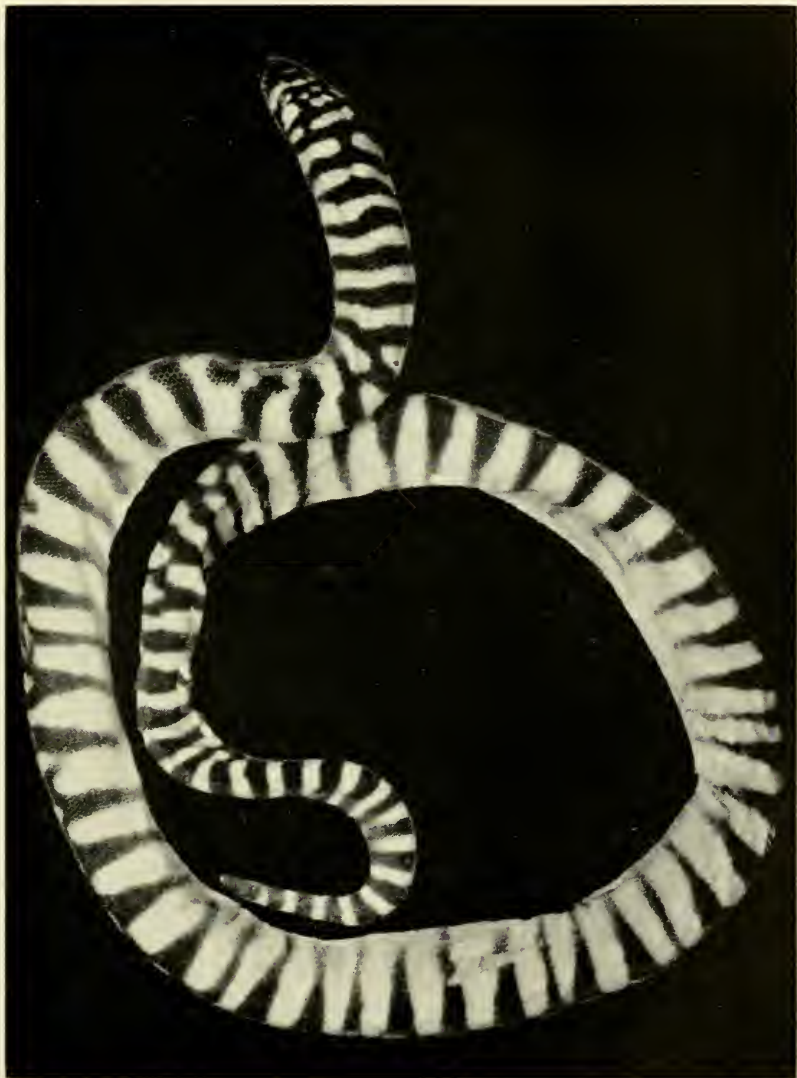


FIG. 24. *Acrochordus granulatus* (Schneider). KUMNH No. 40064 yg., Phet Buri, Thailand. Actual total length, 283 mm.

yellow spots on scalerow 4 and 5, and the yellow border on the nape may be chevron-shaped the apex pointing backwards."

Bourret has listed three forms of *Sibynophis* for French Indo-China, two of which, *sinensis* and *grahami*, are regarded as subspecies of *collaris*. Both Pope (1935) and M. Smith (1943), however, have regarded these as of specific rank. In either case they are not to be confused with the form here described.

SUBFAMILY ACROCHORDINAE

Acrochordus granulatus (Schneider)

Hydrus granulatus Schneider, *Historiae Amphibiorum naturalis et literariae*, fasc. primus, 1799, pp. 243-244.

Three specimens of *Acrochordus granulatus* (KUMNH No. 40064-40066 are from Phet Buri, Thailand, collected by Dr. Boonsong Lekagul. One of the two smaller specimens (No. 40065) differs rather considerably by having the body much compressed and proportionally higher than the others, the black and cream bands of nearly equal width and extending completely around the body. The scalerows at the widest part of the body number from 130 to 140.

The largest specimen, No. 40066, has 53 black bands on body and 13 on the tail. The black bands are widened dorsally and narrowed somewhat laterally.

No. 40064 is longer and slenderer than 40065, the largest number of scalerows about the body being 103. There are 62 dark bands about the body, 13 on the tail, the bands narrowing and fading on the sides, and in some cases not crossing the venter. The body is less compressed than in No. 40065. In all three specimens there are eleven or twelve scales in a row between the eyes.

SUBFAMILY COLUBRINAE

Elaphe radiata (Schlegel)

Coluber radiatus Schlegel, *Essai sur la physionomie des serpens*, vol. 2, 1837, p. 135, pl. V, figs. 5, 6 (type locality, Java); Smith, *Fauna of British India, Ceylon and Burma; Reptilia and Amphibia*, vol. 3, *Serpentes*, Dec. 1943, pp. 146-148, text figs. 44 a, b, c, d, and 46.

The following specimens are in the collections: KUMNH No. 31445, Khorat (city and province), Thailand, Aug. 17, 1953, Robert E. Elbel coll. 31430 (RE 969) Khon San (village), Phukhiao (district), Chaiyaphum (province), Thailand, R. E. Elbel coll. Dec. 25, 1952. 40073 * "Thailand"; 40074, Phukhiao (district), Chaiyaphum

* This appears to be RE 950 Khon San (village), Phukhiao (district), Chaiyaphum (province), Thailand, Dec. 23, 1952, R. E. Elbel coll. The tag is lost.

(province), Thailand, 1952; 40075 yg. (bad state), Kok Kong (village), Chanuman (district), Ubon (province) "from sand by Mekong River," May 31, 1954. R. E. Elbel coll. EHT-HMS No. 31719 (RE 5609), Phu Nam Lang (mt.), elev. 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 10, 1953. R. E. Elbel coll.

The following table shows variation in our series.

Table of data on *Elaphe radiata* (Schlegel)

Number	Total length	Tail length	Ventrals	Subcaudals	Supralabials	Scale-rows	Maxillary teeth	Infra-labials
31430 ♂	1457	276	231	97	9-9	19-19-17	23	10-10
31445 ♂	1320	252	236	98	9-9	19-19-17	22	10-11
31719 ♂	1840	358+	232	90+	8-9	19-19-17	22	10-10
40073 ♂	?	296	...	97	9-9	19-19-17	21	10-10
40074 ♂	1845	362	238	101	9-8	19-19-17	21	11-10
40075 ♀ yg.	...	...	...	...	9-9	19-19-17	21	9-9

This form may be readily diagnosed by the four black lines on the anterior part of the body beginning on the neck some distance back of the head. The posterior part of the body is nearly uniform fawn or sometimes light olive. There are three radiating lines, one below, two behind the eye, the upper touching a transverse black postparietal line, from both ends of which narrow black lines run back to connect with black spot on the side of the neck.

Ptyas mucosus (Linnaeus)

Coluber mucosus Linnaeus, Mus. Ad. Frid. I, 1754, p. 37, pl. 23; Systema Naturae, 10th ed., 1758, p. 226 (type locality, India).

The specimen, KUMNH No. 31444 (RE 723), is from Lam Phaya (village), Nakhon Pathom (district and province), Thailand, collected Apr. 18, 1952 by Robert E. Elbel.

The following characters obtain: supralabials, 7-8, with third and fourth, or fourth and fifth entering eye; 9-9 infralabials; ventrals, 199; subcaudals, 117; scale formula, 23 (head), 17, 15, 17. There are 32 tail bands, the last four or five touching a continuous dorsal line; labial sutures black; head brown; scales with two apical pits. Maxillary teeth 10 + 2 grooved fangs.

A second young specimen is KUMNH No. 40070 (BL 20148) from Thailand without specific locality data from the Dr. Boonsong Lekagul collection. Ventrals, 197; subcaudals, 120; scale formula, 25, 17 (18) 16 14. There is faint indication of keels on the posterior part of the body. There are light black-edged bands on latter half of the body the black continued on venter as black edges on ventrals. The anterior part of the body is nearly uniform olive (olive brown in preservative).

Ptyas korros (Schlegel)

Coluber korros Schlegel, Essai sur la physionomie des serpens, vol. 2, 1837, p. 139 (type locality, Java).

Four specimens of this species are in the collection, KUMNH No. 31434 (RE 951) from Khon San (village), Phukhiao (district), Chaiyaphum (province), Dec. 24, 1952; No. 31446 (RE 998), 6 km. N Chaiyaphum (city), Chaiyaphum (district and province), Jan. 3, 1953, and KUMNH No. 40080 (RE 3644), Ban Hua Bua (subvillage), Um Mao (village), Yangtalat (district), Kalasin (province), all collected by R. E. Elbel, May 6, 1954; KUMNH No. 40069 (BL 20040) "Siam", Dr. Boonsong Lekagul coll.

Table of data for *Ptyas korros*

Number	Sex or age	Ventrals	Subcaudals	Scalrows	Snout-vent length	Tail length
31434	♀	177	141	15, 13, 11	935	533
31446	♀	170	153	15, 15, 11	1036	?
40069	yg	171	127+	15, 16, 11	329	143
40080	♂	163	?	15, 15, 11	1100	?

Lycodon capucinus Boie

Lycodon capucinus Boie, Isis, 1827, p. 551 (based on Russell, Indian Serpents, vol. 2, pl. 37, (type locality Trivandrum, India).

One typical specimen, BL coll. No. ? Rat Buri, Thailand, was examined. We do not regard this as a subspecies of *Lycodon aulicus* (Linnaeus) since each of these forms occupies a large part of the range of the other.

Oligodon cyclurus (Cantor)

(Fig. 25)

Coronella cyclurus Cantor, Proc. Zool. Soc. London, 1839, p. 50 (type locality, ?); M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 4, 1920, p. 96.

Simotes fasciolatus Günther, Reptiles of British India, 1864, p. 218, pl. XX, fig. B (type locality "Petchabun," SE Siam).

Simotes smithi Werner, Sitz. Akad. Wiss. Wien, vol. 143, p. 58 (type locality, Siam).

The several varieties of this species were regarded by Malcolm Smith (1943) merely as color varieties that intergrade with one another. Certain of these variations are represented in the few specimens in the collections as follows:

KUMNH No. 31429 (RE 909), ♀ from Ban Lat (subvillage), Ban Kaeng (village), Phukhiao (district), Chaiyaphum (province), Thailand, Dec. 16, 1952, Robert E. Elbel, coll. This specimen has the following characters: supralabials, 8-8, the fourth and fifth border orbit; infralabials, 9-9; scale formula, 26 (head), 21, 21, 17; ventrals, 175, somewhat angulate laterally; subcaudals, 43; the anal

single; two pre- and two postoculars; temporals, $2 + 2$; 10-9 maxillary teeth, three enlarged.

The triangular head markings are rather narrow, not drawn out anteriorly. The body markings are as follows: the thirteen black circular spots are separated from each other by three dark blotches or marks, the median one most distinct; two circular spots on tail.



FIG. 25. *Oligodon cyclurus* (Cantor). KUMNH No. 40067 "Thailand."
Actual total length, 510 mm.

A row of small dark spots on the fourth and fifth scalerows; immaculate below except for some pigment on the outer edges of the ventrals. This color variety differs somewhat from those listed by Smith (1943, pp. 202-206).

EHT No. 31700 ♂ (RE 4215) from Ban Na Muang (subvillage), Na Haeo (village), Dan Sai (district), Loei (province), Thailand,

elev. approx. 1780 m., Oct. 23, 1954, collected by Robert E. Elbel, gives the following scale data: supralabials, 8-8; infralabials, 9-9; scalerows, 24 (head), 21, 21, 17, 15; scales smooth without pits; temporals, 2 + 2; frontal six-sided; preoculars, 1-2; postoculars, 2-2; loreal present; ventrals, 185; subcaudals, 56; anal single.

EHT-HMS No. 31701 (RE 3909), from Phu Kho (mt.) 522 m. elev., Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, July 24, 1954, collected by Dr. Boonsong Lekagul and Robert E. Elbel, yields the following data: supralabials, 8-8, fourth and fifth enter orbit; infralabials, 9-9, four or five touch first chinshields; scale formula, 26 (head), 21, 21, 17, 17; ventrals, 161; subcaudals, 43; anal single; eleven maxillary teeth, last two large; head and neck pattern complete (see Smith, *loc. cit.*, p. 203). Between the ten large brown spots on body there are three, or more rarely four, indefinite transverse lines similar to the figure given by Smith, fig. D, p. 205, but more intense. Venter with some pigment on outer edge of ventrals.

KUMNH No. 40067, "Thailand" and EHT-HMS No. 31702 (RE 3817) from Phu Phan (mt.) 550 m. elev., Sakon Nakhon (district and province), June 28, 1954, R. E. Elbel and Dr. Boonsong Lekagul collectors, are also in the collection.

Table of data from *Oligodon cyclurus*

Number	Scalerows at middle	Ventrals	Sub- caudals	Supra- labials	Infra- labials	Pre- oculars	Post- oculars	Total length	Tail length
31700 ♂	21	185	56	8-8	9-9	1-2	2-2	812	136
31701 ♀	21	161	43	8-8	9-9	2-2	2-2	579	86
31702 ♂	21	166	54+	8-8	9-10	2-2	2-2	...	109
31429 ♀	21	175	43	8-8	9-9	2-2	2-2	685	90
40067 ♂	21	166	54	8-8	9-9	2-2	2-2	510	111

Oligodon cinereus Günther

(Fig. 26)

Oligodon cinereus Günther, Reptiles of British India, 1864, p. 215 (type locality, Cambodia); Smith, Fauna British India, Ceylon and Burma. . . . Reptilia and Amphibia, vol. 3, Serpentes, 1943, pp. 215-217.

Simotes inornatus Boulenger, Jour. Nat. Hist. Soc. Siam, vol. 1, 1914, p. 69 (type locality, Sriracha, SE Siam).

Oligodon violaceus Smith, Jour. Nat. Hist. Soc. Siam, vol. 4, 1920, p. 96.

One specimen in the collection, EHT-HMS No. 31699 ♀ (RE 4532), resembles the body pattern of Malcolm Smith's var. II, *loc. cit.*, 1943, p. 216. It is from Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, Jan. 20, 1955, Robert E. Elbel, coll. The following characters obtain: 8-7 supralabials, the fourth and fifth or the third and fourth entering eye (the third and fourth fused on one side); temporals, 2 + 2; two

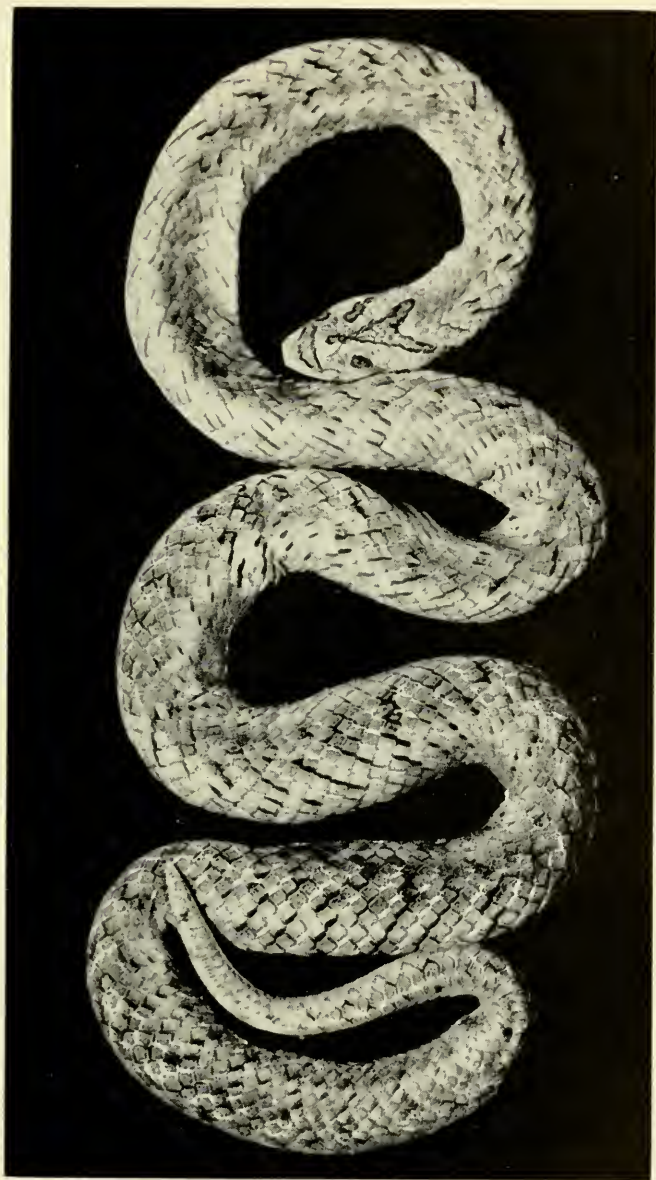


FIG. 26. *Oligodon cinereus* Günther. EHT-HMS No. 31699 ♀, Ban Muang Khai, Tha Li, Tha Li (district), Loei (province), Thailand. Actual total length, 600 mm.

preoculars, the lower much smaller than upper, which is quadrangular, more than twice as wide as high; scale formula, 19 (head), 17, 17, 17, 15; ventrals, 190; subcaudals, 39; anal single; 12 maxillary teeth.

The general color is dark gray with a series of diagonally placed, dotted dark lines often discontinuous along the edges of diagonal scalerows or on skin between; alternate scalerows have a dashed cream line along their edges often extending on the skin between. Tail with two or three indefinite small spots but the characteristic markings of body are absent. The ventrals are generally white with their outer ends dark gray or ash, and with large black spots on alternate ventrals. The subcaudals are white except on the ends and there are no spots evident. A well-defined interocular band is present.

Oligodon quadrilineatus (Jan)

(Fig. 27)

Simotes quadrilineatus Jan, Nouv. Arch. Mus. Paris, vol. 2, pt. 7; Iconographie général des ofidiens, tome 1, livr. 12, 1865, pl. 4, fig. 3 (type locality, Siam); Smith, The Fauna of British India, Ceylon and Burma; Reptilia and Amphibia, vol. 3, Serpentes, Dec. 1953, p. 210.

Simotes taeniatus Boulenger, Catalogue of the snakes in the British Museum (Natural History), vol. 2, pp. 227-228 (*part.*).

The name *Oligodon quadrilineatus* was resurrected by Malcolm Smith in 1943 for this species. It had long been considered a synonym of *O. taeniatus*. The two specimens in our collection help confirm the distinctness of *quadrilineatus*. These are KUMNH Nos. 40068, from Thailand (probably from near Bangkok), and No. 31437, from Ban Lat (subvillage), Ban Kaeng (village), Phukhieo (district), Chaiyaphum (province), Thailand, Jan. 17, 1952, Robert E. Elbel, coll.

The general characters of these two specimens, Nos. 31437 ♀ and 40068 ♂ respectively, are as follows: supralabials, 7-8, 8-8; infra-labials, 9-9, 9-9; labials enter orbit, 4th & 5th, 4th & 5th; preoculars and postoculars, 1-2, 1-2; scale formula, 22 (head), 19, 19, 17, 15; 22, 19, 19, 17, 15; suboculars, 0, 0; temporals, 1 + 1 + 2, 1 + 1 + 2; ventrals, 161, 151; subcaudals, 40, 44; anal, 1, 1. Total length in mm.: 354, 411; tail, 56, 68.

The specimens also agree in color. There is a pair of dark lines dorsally, separated by a narrow lighter line less than the width of a scalerow. The two dark lines meet on the nape of the neck, then widen, terminating on the parietal. On the head a pair of dark diagonal stripes run from the parietal across the angle of the mouth and there are two or three other transverse stripes across the snout.

Some scattered small dark marks are present on the head scales, including a diagonal line below the eye and a shorter one following it behind. The dorsal ground color is grayish tan. A narrow lateral brown line covers parts of the third and fourth scalerows and terminates at the level of the vent. The median pair of brown lines

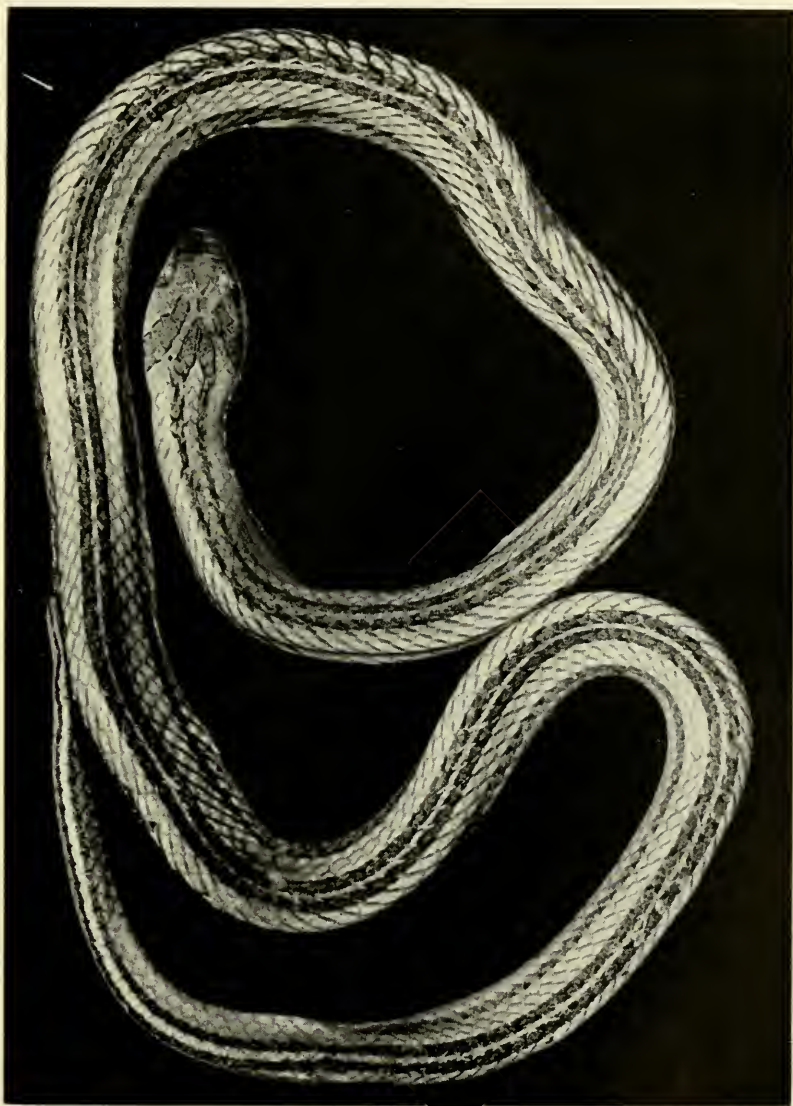


FIG. 27. *Oligodon quadrilineatus* Jan. KUMNH No. 31437, Ban Lat, Ban Kaeng, Phukhieo, Chaiyaphum (province), Thailand. Actual total length, 354 mm.

continues to the tip of the tail. A very indefinite brownish line borders the outer edge of the subcaudals.

The venter is coral red in life (whitish in preservative) with triangular or quadrangular brown marks irregularly placed on ventrals. Usually a scale without marks alternates with one bearing one or two brown spots. The chin and subcaudal regions are immaculate.

Ahaetulla ahaetulla ahaetulla (Linnaeus)

Coluber ahaetulla Linnaeus, *Systema Naturae*, ed. 10, 1758, p. 228 (part).

Ahaetulla ahaetulla ahaetulla Smith, *Fauna of British India, Ceylon and Burma; Reptilia and Amphibia*, vol. 3, *Serpentes*, 1943, pp. 239-244, fig. 85.

There has been very considerable disagreement as to the proper name for this species.* It was long known under the designation *Dendrophis pictus* and so appears in the major part of the literature dealing with the species.

One specimen (KUMNH No. 40076 [RE 1691]) from Pak-nampho (city), Nakhon Sawan (district and province), Thailand, was collected by the junior author.

The following characters obtain: maxillary teeth, 22; the four posterior largest; one preocular touching frontal; two postoculars the upper elongate; supralabials, 9-9, the 4th, 5th and 6th entering orbit; temporals, $2 + 1 + 2$ ($1 + 1 + 2$); one loreal more than twice as long as high; scales following parietals and temporals somewhat enlarged; scale formula, 19 (head), 15, 15, 9; median row enlarged but definitely somewhat less wide than outer scalerow. The ventrals are $172\frac{1}{2}$; subcaudals 130, anal divided. Scales with a single apical pit, the surface of the epidermis finely striate, not discernible when epidermis is shed.

There is a strong black line from behind eye onto neck; a cream line on the two outer scalerows with a well-defined dark line below it covering part of outer scalerow and outer edge of the ventrals. Type locality unknown.

SUBFAMILY BOIGINAE

Boiga multimaculata (Boie)

Dipsas multimaculata Boie, *Isis*, 1827, p. 549 (type locality, Java).

Our specimen, KUMNH No. 31439 (RE 890), is from Non Khun (village), Phukhiao (district), Chaiyaphum (province), Thailand; collected Dec. 12, 1952, by Robert E. Elbel.

* Besides Malcolm Smith, *loc. cit.*, see also discussion by James Oliver, *Bull. Amer. Mus. Nat. Hist.*, vol. 92, art. 4, 1948, pp. 167-190, 267-272; J. M. Savage, *Bull. Chicago Acad. Sci.*, vol. 9, 1952, pp. 203-216.

This specimen has the following scale counts: supralabials, 8-8, the third, fourth and fifth entering the eye; infralabials, 11-11; preocular, 1; postoculars, 2; temporals, 2 + 2; scale formula, 27 (head), 19, 19, 13; ventrals, 223; anal single; subcaudals, 99. Body slender, compressed. Total length, 565 mm.; tail, 113 mm.

Two dark stripes begin on the posterior temporal areas and run forward diagonally and meet on the anterior part of the frontal, continuing on to the middle of the prefrontals; a dark stripe from angle of mouth runs forward to eye, and then continues in front of eye to nasal scale. Back and tail with a series of dark brown spots, often irregular in outline, running from neck to tail, separated mesially by a narrow line of the gray of the general coloration. Chin unspotted; anteriorly, dark marks present on outer part of ventrals; more posteriorly the flecks become more numerous extending over whole ventral region.

Boiga cyanea (Duméril, Bibron and Duméril)

(Fig. 28)

Triglyphodon cyaneum Duméril, Bibron and Duméril, *Erpétologie générale*, vol. 7, pt. 2, 1894, pp. 1079-1080 (type locality unknown).

Two specimens are at hand, EHT-HMS No. 31693 (RE 4016) from Ban Na Muang (subvillage), elev. approx. 1780 m. "in same range as Phu Nam Lang (mt.) but farther north," Na Haeo (village), Dan Sai (district), Loei (province), Thailand; Sept. 29, 1954, Robert E. Elbel coll., and EHT-HMS No. 31826 (RE 4689) from Phu Lom Lo (mt.), elev. 2100 m., Kok Sathon (village), Dan Sai (district), Loei (province), Feb. 18, 1955, R. E. Elbel, coll.

No. 31693 ♀ has the following characteristics: supralabials, 8-8; the third, fourth, and fifth entering eye; infralabials, 11-11, four (or five) touching first pair of chinshields; one preocular, reaching upper surface of head but not touching frontal; eye very large, its diameter equal to its distance from nearest point of rostral; two postoculars; temporals, 3 + 3 (median divided) + 4 on both sides; scale formula, 29 head, 21, 21, 15, 15, and the median row somewhat enlarged; ventrals, 248; subcaudals, 136; anal single. Body compressed. The subcaudals have an indistinct lateral keel; no gland visible through the posterior labials. Total length, 1558 mm.; tail, 311 mm.

The color was probably uniform green in life. In preservative it is bluish to bluish gray, the edges of the scales darker. The chinshields are cream.

No. 31826 is a young specimen and we are not wholly convinced that it is correctly referred to this species. The following characters obtain: supralabials, 8-8; the third, fourth, and fifth entering orbit;

11-11 infralabials, four touching first chinshields; one preocular reaching upper surface of head, but not touching frontal; scale formula, head 28, 22, 21, 15, the median row somewhat enlarged; ventrals, 250; subcaudals, 124, with an elongate terminal shield,

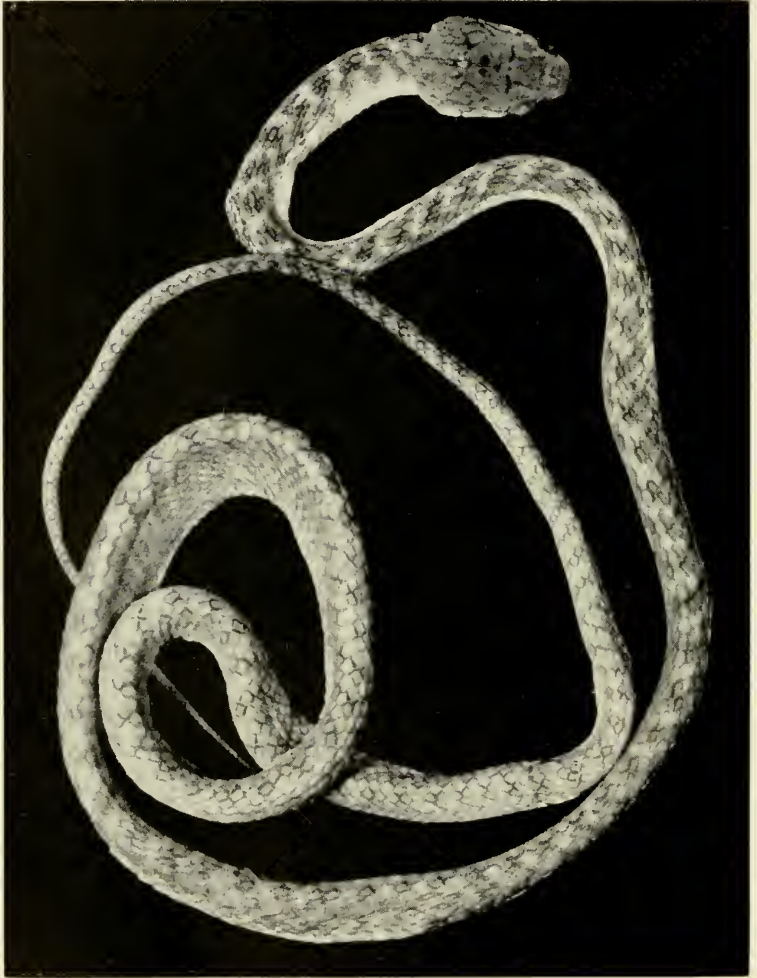


FIG. 28. *Boiga cyanea* (Duméril, Bibron and Duméril). EHT-HMS No. 31826, Phu Lom Lo (mt.), 2100 m. elev., Kok Sathon, Dan Sai, Loei (province), Thailand. Actual total length, 700 mm.

rounded at tip, grooved on both sides; anal single; temporals, $2 + 3 + 3$ ($2 + \frac{1}{2} + 3$); loreal as high as long; total length, 720; tail, 161 mm.

The head is uniform smoky black, probably green in life; three posterior supralabials semitransparent showing a cream-colored gland lying below them. Body with dark markings as shown in the figure.

The species has been reported from Nakon Lampang, Dong Rek Mts., and from certain islands in the Gulf of Siam.

Malcolm Smith and others have pointed out that the young are not green but are variously colored and marked. The squamation is practically identical to that of the adult specimen reported above. One specimen examined in the Boonsong Lekagul collection (No. 222) is from Khao Khansong (village), Sriracha (district), Chon Buri (province), Thailand, Aug. 1953, Dr. Boonsong Lekagul, coll.

Boiga cynodon Boie

Boiga cynodon Boie, Isis, 1827, p. 549 (type locality, Sumatra).

Our single specimen is EHT-HMS No. 31698 (RE 4099), from Ban Na Muang (subvillage, elevation 1780 m.), Na Haeo (village), Dan Sai (district), Loei (province), Thailand; October 6, 1954, Robert E. Elbel, coll. The following characters obtain: supralabials, 8-8, the third, fourth and fifth entering orbit; infralabials, 12-12, the first four (or five) touching the first pair of chinshields; second chinshields larger than first pair; frontal broader than long; eye equals its distance from nostril; temporals, 2 + 3, 3 + 3.

Scale formula, (head) 26, 23, 23, 15, 15; ventrals, 261, anal single, subcaudals, 118. Maxillary teeth, 11 + 2 grooved fangs.

Above clouded and indefinitely blotched with brown, fawn, and black. A series of light (fawn) blotches low on the sides surrounded by black, situated chiefly on the outer part of ventrals. Remainder of venter gray-brown.

Dryophiops rubescens (Gray)

Dipsas rubescens Gray, Illustrations of Indian Zoology, vol. 2, 1834, pl. 84, fig. 2 (type locality, ? Malay Peninsula).

One specimen seen is BL Coll. No. 20099, collected by Dr. Boonsong Lekagul, from "Siam." This widespread, usually arboreal species is relatively rare in collections. The senior author has taken it on Peñon de Corón, western Philippines, a limestone island covered sparsely with small shrubs and plants, but lacking trees owing to the almost complete absence of soil on the rock.

Psammodynastes pulverulentus Boie

Psammodynastes pulverulenta Boie, Isis, 1827, p. 547 (type locality, "Java").

This variable and widespread form is represented by three specimens: EHT-HMS No. 31793 (RE 3817), from Phu Phan (mt.) 550 m. elevation, Sakon Nakhon (district), Sakon Nakhon (province), Thailand; collected by Dr. Boonsong Lekagul and Robert E. Elbel June 28, 1954. No. 31794 (RE 4689), a beheaded specimen, Phu Lom Lo (mt.) 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Thailand; Feb. 18, 1955, Robert E. Elbel, coll. No. 31795 (RE 5002), Phu Nam Lang (mt.) 1780 m. elev., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, 1955, R. E. Elbel, coll.

No. 31794 ♀ had recently eaten a young *Eumeces quadrilineatus*. The specimen is gravid, containing seven eggs. There are 49 subcaudals and 17 scalerows.

The following scale data are taken from No. 31795 ♀: supralabials, 8-8; infralabials, 8-8; five pairs of chinshields, the second and third about equal, three infralabials touching the first pair; one loreal, two pre- and two postoculars; supraoculars wider than frontal; ventrals, 163; subcaudals, 53; anal single; scalerows, head, 25, neck, 17, body, 17, in front of tail, 17, all without pits.

No. 31793 ♀ has the following scale counts: supralabials and infralabials, 8-8, the third, fourth, and fifth supralabials border orbit; three infralabials touch the first chinshields; one preocular; two postoculars; the temporals, 2 + 3 + 3. The second and third pairs of chinshields are longer than the first; scalerows, 24, 17, 17, 15; ventrals, 149; subcaudals, 52. The maxillary teeth vary greatly in size, the last two being grooved.

The species occurs also in Indonesia, and the senior author has collected it in the mountains of central eastern Mindanao, P. I.

Chrysopelea ornata (Shaw)

Coluber ornatus Shaw, General Zoology, 1802, vol. 3, p. 477 (type locality, East Indian Islands, based on Seba, Thesaurus, vol. 1, pl. 94, fig. 7; vol. 2, pl. 7, fig. 1 and pl. 61, fig. 2).

Chrysopelea ornata Brongersma, Zool. Meded. Leiden, vol. 20, 1938, p. 241; M. Smith, The fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region; Reptilia and Amphibia, vol. 3, Serpentes, Dec. 1943, pp. 251-254, text figs. 86, 87.

Two forms of the arboreal *C. ornata* are recognized by Malcolm Smith, one occurring in Thailand, one in Ceylon and India.

The former is characterized as having "the black cross-bars much less conspicuous and may be entirely absent; the mesial streak on

each scale may then give the appearance of black longitudinal lines." The head markings consist of five or six golden yellow transverse bars following scale sutures between rostral, internasals, prefrontals, frontal and following parietal while one crosses the middle of the frontal. There are usually several golden dots between the lines. The lines may be apparently broken when crossing longitudinal sutures. In the latter form the black and yellow bars alternate.

Five specimens are at hand in the collection as follows: KUMNH Nos. 31431 (RE 1600), Paknampho (city), Nakhon Sawan (district and province), Thailand, Jan. 18, 1953, and 31432, Banpong (city and district), Rat Buri (province), June 16, 1952, both collected by Robert E. Elbel.

EHT-HMS Nos. 31817 (RE 3756), Phu Phan (mt.), 550 m., 104° 05'; 16° 55', Sakon Nakhon (district and province); 31818 (RE 3846), Phu Kho (mt.), circa 522 m. elev. (104° 22'; 16° 49'), Kan Luang (village), Na Kae (district), Nakhon Phanom (province). Collected June 20 and July 16, 1954, respectively by Dr. Boonsong Lekagul and Robert E. Elbel.

In the form occurring in Thailand the row of scales bordering the parietals and temporals behind are definitely enlarged; the ventrals, anals, and subcaudals are strongly keeled; in the region on sides and above anus the scales are usually more or less keeled. In all there are two postoculars, the temporals, 2 + 2 + 2, and the scalerows are 24 (25) head, 17, 17, 13. The infralabials are ten or eleven with five scales usually bordering the first chinshields.

Chrysopelea paradisi occurs in the peninsular area of Thailand, and also in Indonesia and the Philippines.

Scale data on Chrysopelea ornata Shaw

Number	Sex	Preocular	Preocular reaches frontal	Ventrals	Subcaudals	Anals
31817	♀	1-1	no	218	107+	2 2 ½
31818	♀	1-1	no	222	117	2 2 (?)
31819	♂	1-1	yes	223	138	2 2
31431	♂	1-1	no	224	141+	2 2
31432	♂	1-1	no	222	140	2 ½ 2

Dryophis prasinus Boie

Dryophis prasinus Boie, Isis, 1827, p. 545 (type locality, Java); Malcolm Smith, Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region. Reptilia and Amphibia, vol. 3, Serpentes, Dec. 1943, pp. 375-386, text fig. 120.

Malcolm Smith's (*loc. cit.*) treatment of the genus calls attention to the fact that *Dryophis xanthozonia* Boie should bear the name

Dryophis mycterizans (Linnaeus) while the species long known in literature under the latter name should bear the name *Dryophis pulverulentus* Duméril and Bibron and Duméril. This is mentioned here since *mycterizans* occurs in Thailand also. It may be separated from the present species by its undivided anal plate, fewer ventrals * and subcaudals.

A single specimen of *Dryophis prasinus*, KUMNH No. 40077 (RE 3474) is in the collection. It was captured on Phu Lom Lo (mt.) 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Mar. 26, 1954, by Robert E. Elbel.

The following characters obtain: no proboscis, the nasals not in contact; sharp canthus; nasal single, elongate, the nostril in posterior part; two or three loreals separate prefrontals from labials; one preocular, longer than high, with a sharp canthus, broadly touching the frontal; supralabials, 9-9, the fourth, fifth and sixth enter orbit; two postoculars; frontal three times as wide anteriorly as posteriorly; temporals $2 + 2 + 3 + 3$, the lower anterior very small; anterior chinshields broader and shorter than the very narrow posterior ones; infralabials, 9-9, the first four touch first chinshields.

Scale formula: 21 head, 15, 15, 11, the scales in the region of vent with keels or tubercles, the middle line of the scales with series of pits, four to five on some scales. Ventrals ? (body broken); subcaudals, 196; anal divided.

Dryophis nasutus Lacépède

Dryophis nasutus Lacépède, Histoire naturelle des serpens, vol. 2, 1789, Discourse and Table Methodique, p. 100. Also, pp. 277-279, pl. 4, fig. 2 (type locality, Ceylon, Guinea, Carolina); Smith, The fauna of British India, Ceylon and Burma, including the whole Indo-Chinese subregion. Reptilia and Amphibia, vol. III, Serpentes, Dec. 1943, pp. 376-378 (synonymy and literature), fig. 119 (head, three views).

Of the type localities listed by M. le Comte de Lacépède for this species, one only, Ceylon, has the species. In consequence the locality Ceylon is hereby designated as the revised type locality.

One specimen, KUMNH No. 31438 (RE 783) from Paknampho (city), Nakhon Sawan (district and province), Thailand, Jan. 30, 1953, Robert E. Elbel, collector, is in the collection. There are 202 ventrals, the last (preceding divided anal) also divided. The divided anal has a small intercalated median scute which may be an abnormality. The subcaudals are 163. The scalerows about the back part of the head are 20, about neck 15, about middle of body

* 186-195 ventrals, 132-156 subcaudals *vide* Malcolm Smith while *prasinus* has 194-235 ventrals, 165-187 subcaudals *vide* Malcolm Smith.

15, while in front of anus the number reduces to 11. There are two pre- and two postoculars.

The tooth series on the maxillary consists of three spaced teeth anteriorly followed by a fanglike tooth, which, after a diastema, is followed by four small teeth, and two enlarged grooved fangs.

The nasal appendage is formed entirely from the rostral. The loreal is absent.

Total length, 662 mm.; tail, 227 mm.

SUBFAMILY NATRICINAE

Pseudoxenodon macrops macrops (Blyth)

(Fig. 29)

Tropidonotus macrops Blyth, Asiat. Soc. Bengal, vol. 23, 1854, p. 296 (type locality, Darjeeling, Bengal, India).

Two specimens are in the collection: EHT-HMS No. 31703 (RE 4521) is from Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, Jan. 19, 1955, and EHT-HMS No. 31704 (RE 5533) juv., Phu Nam Lang (mt.), (elev. 1780 m.), Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 4, 1955; both collected by Robert E. Elbel.

There is a series of white (?) transverse bands across the mid-line extending throughout the body to the tip of the tail, the edges of each band in front and behind bordered by large dim dark spots formed of scales with black edges and grayish centers. Laterally the light bands terminate at black spots which form a row on the third to fifth scalerows. The space on the dorsal area between each two dark spots may be light (whitish) but is never as distinct as the primary white marks. There are quadrangular dark spots on the ventrals.

The following scale characters obtain: scalerows, 19, 15, 15; anterior temporals, 2; supralabials, 8; infralabials, 8; ventrals, 171; subcaudals, 63; anal, 2.

The young specimen has 174 ventrals and 67 subcaudals. The supralabials are 8-8, with dark sutures. The infralabials are 9-9. On the back there are 50 white transverse spots. The black chevron on the neck is preceded by a lighter line. Total length, No. 31793: 882 mm.; tail, 160; No. 31704: 263 mm.; tail, 47.5.

The larger contains 10 ovarian eggs.

Genus NATRIX

The genus *Natrix* is a heterogeneous assemblage and efforts to break up this unnatural group have not been successful. One group of species, characterized by very long posterior ungrooved fangs, is thrown in with species having little or no enlargement of the

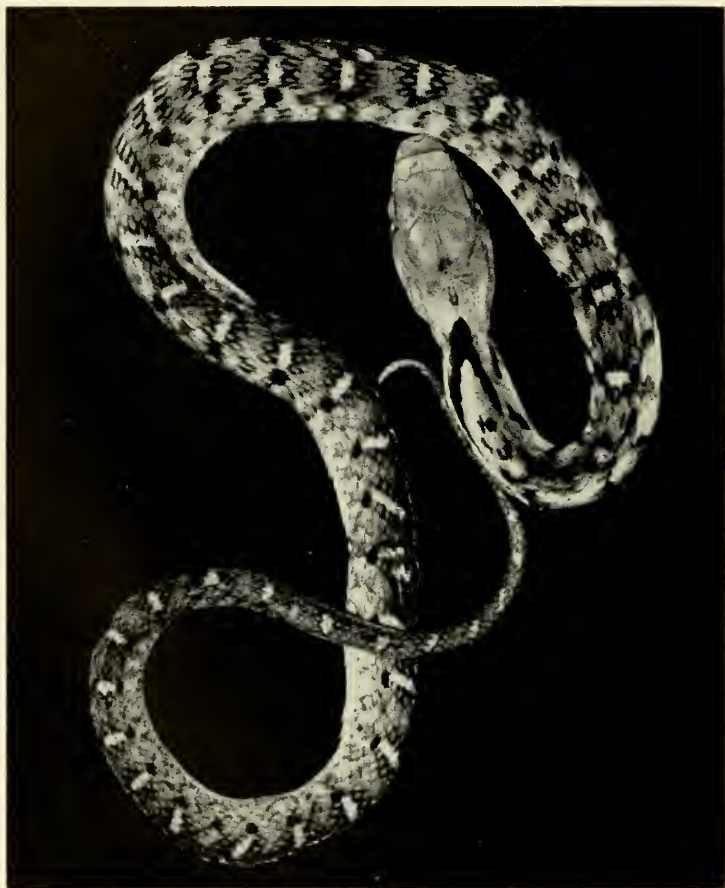


FIG. 29. *Pseudoxenodon macrops macrops* (Blyth). EHT-HMS No. 31704, Phu Nam Lang (mt.), 1780 m., Ban Khok, Na Phung, Dan Sai, Loei (province), Thailand. Actual total length, 263 mm. (Note that the head is proportionally large in this young specimen.)

posterior teeth. We are of the opinion that the entire matter is in strong need of re-examination.

In this paper we propose to recognize the large-fanged species under the generic name *Rhabdophis*. The following species of

Natrix (*sensu lato*) have been reported in Thailand: *deschauenseei*, *groundwateri*, *inas*, *modesta*, *piscator piscator*, *trianguligera*, *percarinata*, *subminiata subminiata*, *subminiata helleri*, *stolata*, *nigrocincta*, *chrysarga*. The last five forms are typical *Rhabdophis*, *R. subminiata* being the type of the genus. Certain other forms reported from Thailand may be misidentifications or are synonyms. Such a case is Bourret's *Rhabdophis tigrina lateralis* which Malcolm Smith places as a synonym of *piscator*.

Natrix deschauenseei, described by the senior author from Chiang Mai, Thailand, has also been placed as a synonym of *Natrix modesta* by Dr. Malcolm Smith. It, however, seems to differ from that Indian species in having 36 maxillary teeth (28 to 32 recorded for *modesta*); nasal divided; two preoculars, two postoculars (usually three); temporals, 1 + 2; only two (fifth and sixth labials) entering orbit instead of three; ventrals, 159, subcaudals, 137—total, 296, higher than reported for *modesta*. The body is very slender with a proportionally longer tail. The color pattern differs likewise in details (see figures of the type and compare with Boulenger, vol. 1, pl. 9, fig. 3). Dr. Smith states that he has not seen a specimen of *deschauenseei*. It is possible that collections from the region of Chiang Mai, the type locality, will provide data suggesting the distinctness of the species or confirming Dr. Smith's opinion as to synonymy. No material is available in this collection. Bourret has placed the species in the genus *Macropophys* Boulenger.

Natrix piscator flavipunctata (Hallowell)

Amphiesma flavipunctatum Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 503 (type locality, Kwantung province, China).

Two specimens are referred to the subspecies *Natrix piscator flavipunctata*: KUMNH No. 31441 ♂ (RE 965), Khon San (village), Phukhiao (district), Chaiyaphum (province), Thailand, Dec. 24, 1952; No. 31440 ♂ (RE 967), same locality, Dec. 25, 1952. Robert E. Elbel, collector.

The following characters obtain in the two specimens, 31441 and 31440 respectively: snout pointed; internasals pointed anteriorly; body with a tendency to form a slight median ridge; supralabials, 9-9, 9-9; labials entering orbit, 4 and 5, 4 and 5; 4, 4 and 5; preoculars, 1-1, 1-1; postoculars and suboculars, 3-4, 3-3; infralabials, 10-10, 10-10, five touching the anterior chinshields which are shorter than second pair; scalerows, head, 25, 19, 19, 17; 24, 19, 19, 17; two outer scalerows smooth (3 anteriorly), others weakly keeled;

anterior temporals, 2, 2; ventrals 134 ♀, 127 ♂; subcaudals, 59 +, 85.

The head is black above in No. 31441 the color extending onto the neck; a diagonal black line along suture of sixth and seventh labials; another black line from behind eye runs down across the mouth angle then curves back up onto side of neck bordering the dark head mark; a distinct black spot on each side of the neck. Nearly uniformly lavender-brown with the merest trace of dark markings and numerous dashlike cream or yellow indistinct marks chiefly confined to interstitial skin or edges of scales; ventrals and subcaudals are dark edged. In No. 31440 some lateral dark marks running up on sides diagonally, ventrals and subcaudals cream or whitish, their edges barred with black.

The maxillary teeth in 31441, 24, the last four enlarged and strongly compressed; teeth in No. 31440, 26-24, the last four compressed and enlarged, the last a little larger than the others. There is no diastema between the larger and the smaller teeth.

While we follow Malcolm Smith in treating this form as a subspecific form of *Natrix piscator* there seems room for doubt that this is its true relationship.

Rhabdophis subminiata helleri (Schmidt)

Natrix helleri Schmidt, Amer. Mus. Novitates, no. 157, 1925, p. 3 (type locality, Tengyueh, 5500 ft. altitude, province of Yunnan, China).

The following series of specimens are referred to this form: EHT-HMS No. 31765 (RE 5504), Phu Nam Lang (mt.), 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, 1955; EHT-HMS No. 31766 (RE 4323), 31812 (RE 4311), 31813 (RE 4305), 31814 (RE 4256), 31815 (RE 4256), 31816 (RE 4310)—all from Ban Nong Wai (subvillage), 1780 m., Na Phung (village), Dan Sai (district), Loei (province), Thailand, Nov. 15-20, 1954, all collected by Robert E. Elbel. KUMNH No. 40072 (RE 3189), Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, about 600 m. elev., Dec. 4, 1953; collected by Robert E. Elbel, and Dr. Boonsong Lekagul.

The following table presents data from the above series of specimens.

Data on Rhabdophis subminiata helleri

Number	Sex	Supra-labials	Labials enter orbit	Infra-labials	Maxillary teeth and fangs	Ventrals	Sub-caudals
31766	♂	8-8	4, 5	10-10	{25+2 23+2	155	89+
31811	♂	8-8	3, 4, 5	10-10	22+2	153	84
31812	♀	8-9	{3, 4, 5 4, 5, 6	10-10	22+2	151	84
31813	♀	9-8	{4, 5, 6 3, 4, 5	10-10	22+2	152	78+
31814	♂	8-8	4, 5	9-10	22+2	158	81
31815	♀	8-8	4, 5	10-10	22+2	155	83
31816	♀	8-9	{3, 4, 5 4, 5, 6	10-10	23+2	163	—?

Young specimens have a large discrete black spot covering the back of the head and extending for ten to twelve scale-lengths behind parietals; it is bordered by a lighter line about one and one-half scale-lengths wide. There follow several rows of indefinite dark spots more or less connected and forming a reticulum. The enclosed scales have red interstitial skin, the color sometimes covering more than half of the scale. Farther back the color is uniform gray olive (somewhat blackish in preservative) with usually two series of single or double paired yellow dots on the sides; sometimes these pairs will be connected by small dashlike marks across the back. When the skin is distended more yellow marks are discernible on interstitial skin or on lower edges of scale. A few specimens show traces of black marks usually, appearing as black edges of certain adjoining scales.

The maxillary teeth are small anteriorly gradually attaining a slightly greater size, then, following a short diastema, are two greatly enlarged fangs directed nearly backwards. Ventral coloration is light, probably yellowish (or reddish) in life, the outer edges of the ventrals gray, often with small discrete or diffuse dots near their ends; supralabials light with a strongly defined diagonal bar below back part of eye. Dorsal head markings are dim or obsolete in old specimens.

Rhabdophis stolata (Linnaeus)

(Fig. 30)

Natrix stolata Linnaeus, Systema Naturae, 10th ed., 1758, p. 219 (type locality, Asia).

A single specimen, EHT-HMS No. 31761 ♂ (RE 3952), is from Ban Na Phua (subvillage), Kan Luang (village), Na Kae (district), Nakhon Phanom (province), Thailand, collected July 28, 1954, by Robert E. Elbel and Dr. Boonsong Lekagul. The markings are typical of the eastern (Chinese) specimens. The following

characters obtain: supralabials, 8-8; infralabials, 10-10; temporals, $1 + 1$, or $1 + 2$; scale formula, 19, 19, 17; ventrals, 144; subcaudals, 50; preocular, 1; postoculars, 3; maxillary teeth, $21 + 2$ (enlarged). Snout-vent length, 356 mm.; tail, 92 mm.

There is a light chevron-shaped band across the neck. From this two stripes begin, covering the fifth scalerow and halves of the adjoining rows. These stripes, grayish at first, become white farther back and extend to the tip of the tail.

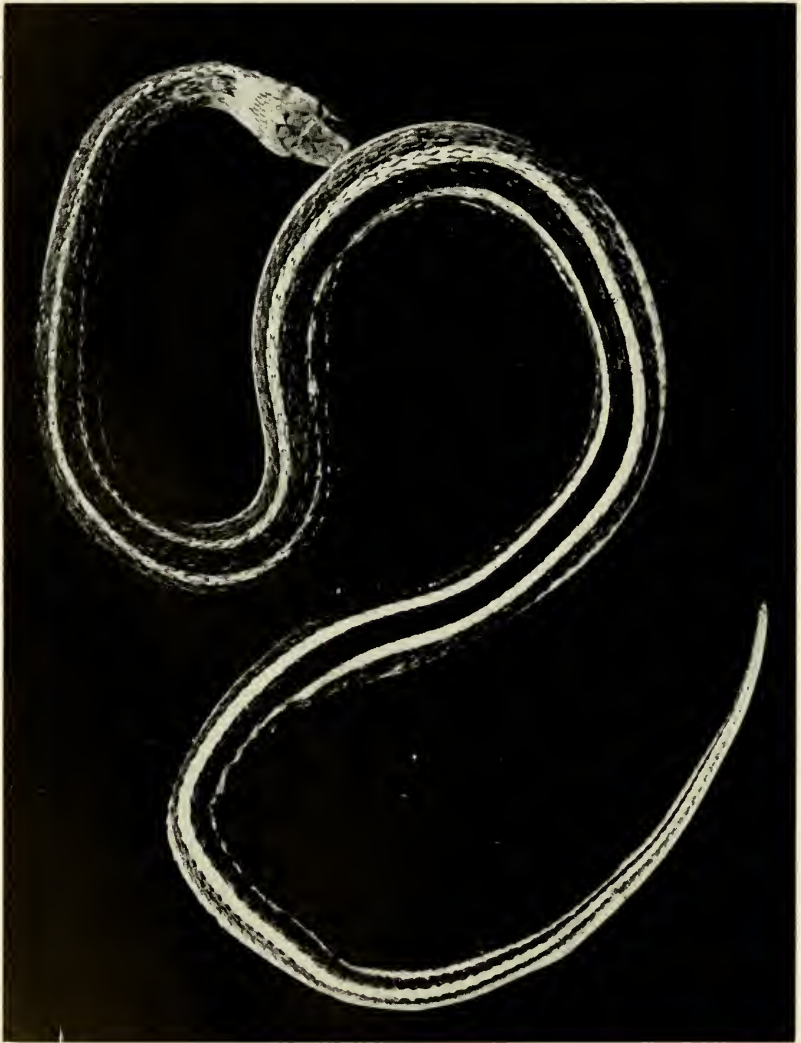


FIG. 30. *Rhabdophis stolata* Linnaeus. EHT-HMS No. 31761, Ban Na Phua, Na Kae, Nakhon Phanom (province), Thailand. Actual total length, 448 mm.

Rhabdophis nigrocincta (Blyth)

Tropidonotus nigrocinctus Blyth, Jour. Asiat. Soc. Bengal, vol. 24, 1856, p. 717 (type locality, Pegu, Burma).

There are two specimens in the collections: EHT-HMS No. 31760 ♂ (RE 5517) from Phu Nam Lang (mt.), 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 3, 1955, Robert E. Elbel, coll.; and KUMNH No. 40071 ♀ (RE 3541) from Phu Lom Lo (mt.), 2100 m. elev., Kok Sathon (village), Dan Sai (district), Loei (province), Thailand, Mar. 30, 1954, Dr. Boonsong Lekagul and Robert E. Elbel, collectors.

The following characters obtain in No. 31760: maxillary teeth, 29-30, followed by two suddenly enlarged fangs lacking grooves, several times larger than nearest tooth; ventrals, 167; subcaudals, 99; anal divided; scale formula, 27 head, 19, 19, 17; scales except outer row keeled; two anterior temporals; one preocular, three postoculars; supralabials, 9-9, the fourth to sixth enter orbit; internasals truncate anteriorly; a distinct series of 8 pairs of nuchal glands; on each side of median line of neck a short indistinct groove. Total length in mm.: 615; tail, 179.

A narrow band (six to eight rows wide) following the parietals is lighter than ground color, suggesting a juvenile light band; this is followed by a deep-black chevron pointing backward; general ground color dark gray with a series of 46 narrow transverse black bars on the body, sometimes broken mesially and alternating; tail banded and flecked with black. Venter with anterior part ivory, the median third gray, the posterior part with dark blackish-gray or brown clouding or blotching; underside of tail dark with white flecks; an immaculate white or cream spot on labials between a diagonal postocular stripe and a short subocular stripe.

No. 40071 is a larger specimen but it is injured anteriorly so that an accurate measurement cannot be made. It agrees in general with the above specimen. There are two anterior temporals, one preocular and four postoculars; 9-9 supralabials, 10-11 infralabials, five or six bordering the anterior chinshields which are shorter than posterior; latter separated by small scales; ventrals, approximately, 166, subcaudals, 88; anal divided. Scale formula, 28 head, 19, 19, 17. There are 31 + 2 maxillary teeth.

The stomach contains a specimen of a frog (*Megophrys*) partially digested.

Rhabdophis chrysarga (Schlegel)

Tropidonotus chrysargus Boie, Isis, 1827, p. 534 (Java), *nomen nudum*.
Schlegel, Phys. Serp., vol. 2, 1837, p. 312, pl. 12, figs. 6-7.

A specimen (BL No. 20090 from "Thailand") was examined. This species is widespread, extending through southeastern Asia, Indonesia and into the Philippines.

Parahelicops boonsongi sp. nov.

(Fig. 31)

Holotype: EHT-HMS 31707 (RE 5500), Phu Nam Lang (mt.), 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, 1955; Robert E. Elbel, collector.

Diagnosis: A natricine snake, with 30 maxillary teeth, the last three suddenly much enlarged but not grooved; internasals narrowed; a single prefrontal; three (or two) postoculars; two suboculars; one preocular; nasal partially divided; anal divided; with a divided scale also preceding it; all dorsal scalerows finely striate and heavily keeled, outer ones less so except outermost which is smooth anteriorly and faintly keeled posteriorly; posterior edges of scales notched, bearing a fine transparent fringe. Uniform gray-olive on dorsal parts (in preservative), growing gradually lighter laterally, the outer scalerows almost cream-white anteriorly; venter cream-white or yellowish; subcaudal region gray.

Description of type: Rostral once and a half as wide as high, very narrowly visible above; internasals elongate, narrowed anteriorly, rounded posteriorly, their length slightly greater than length of the prefrontal; latter twice as wide as long; frontal five-sided, slightly wider anteriorly than elsewhere, a little shorter than supraoculars, equal to its distance from rostral, a third shorter than parietals; nasal elongate; a suture from nostril to second supralabial; loreal as high as long; a large preocular not reaching frontal; three postoculars, two suboculars, the anterior reaching forward beyond middle of eye; temporals, 2 + 3 + 4; nine supralabials, the first three touching nasal, third only touches loreal, fourth and fifth enter orbit, seventh largest; mental wider than deep, as wide as rostral; infralabials ten, five touching first chinshields which are distinctly shorter than second pair; latter separated, narrowly so anteriorly.

Scalerows across back of head 25, at neck 19, middle of body 19, in front of vent 17. Ventrals, 141; anals, 2; subcaudals, 33 + (tail

broken and lost). Eye rather large, equal to its distance from nostril; pupil round.

Color: Nearly uniform gray-olive growing a little lighter laterally, becoming nearly cream-white on outer two or three scalerows anteriorly on side of neck; posteriorly two outer scalerows and to some extent the outer edge of ventrals with some grayish pigment; supralabials and suboculars cream; an indefinite fumate spot back

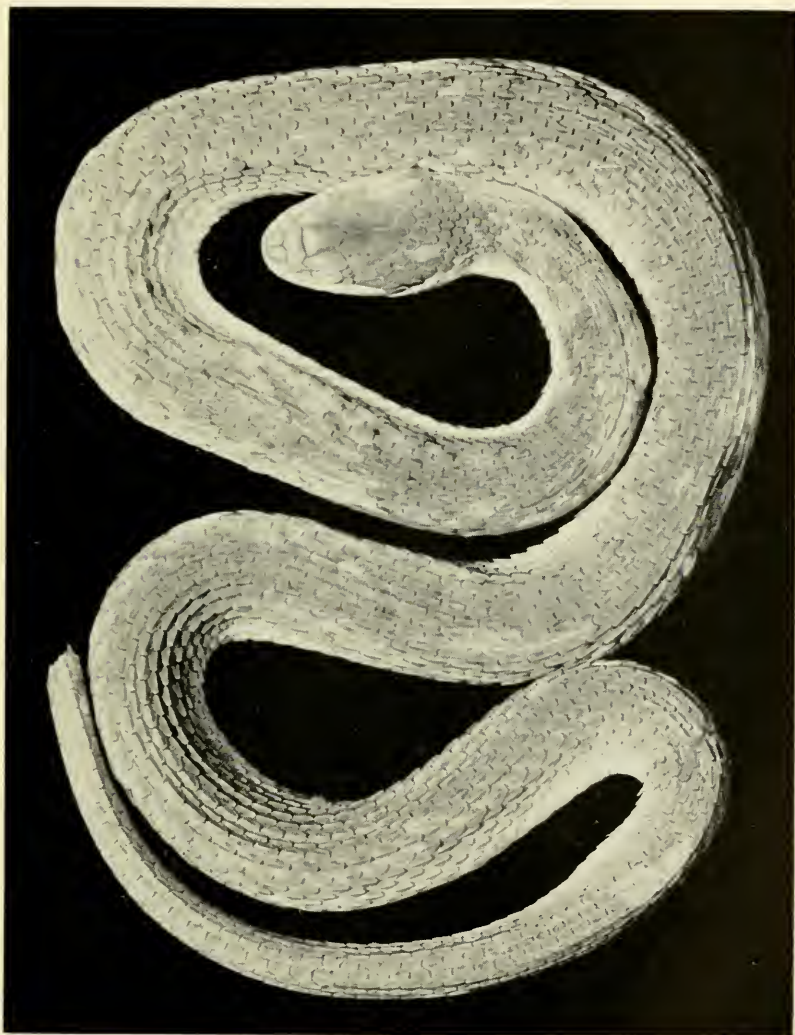


Fig 31. *Parahelicops Boonsongi* sp. nov. EHT-HMS No. 31707, Phu Nam Lang (mt.), 1780 m., Ban Khok, Na Phung, Dan Sai, Loei (province), Thailand. Actual total length 621 mm.

of jaw angle; tail incomplete; venter generally cream-white; subcaudal region with a median gray line and many scales with an indefinite pigmented area (on portion of tail remaining).

When the specimen is held in certain lights or immersed in clear liquid it is possible to discern dimly certain indefinite darker areas on the anterior half of the body.

Measurements in mm.: Snout to vent, 520; tail, 101 +; total length 621 +; length of head, 26; width of head, 18; width of neck, 13.

Remarks: The genus *Parahelicops* was proposed by Bourret for a species having a single prefrontal, the scales lacking apical pits, hypapophyses developed throughout the vertebral column, 25 maxillary teeth, the last two enlarged but not grooved. The present species differs from the described type of the genus *Parahelicops annamensis* Bourret in having a totally different pattern of coloration, more maxillary teeth (30 as compared with 25); the nasal partially instead of wholly divided; the scalerows 19, 19, 17 instead of 17, 17, 15; the anal double (preceded by a paired scale), instead of a single anal; eye larger, and the ventrals 141 (compared with 169 in *annamensis*). The character of the temporals (abnormal in *annamensis*) are 2 + 3 + 4 (as compared with 1 + 1 + 2 on the normal ? right side while on the left side there is one long fused scale followed by three). There are three instead of one (or two) suboculars.

The species is named for Dr. Boonsong Lekagul who has so generously provided the University of Kansas with Thailand amphibians and reptiles.

Pope (Rept. China, 1936, p. 125, and M. Smith, vol. 3, Fauna Indian Reptilia and Amph., 1943, p. 330), have placed *Parahelicops* in the synonymy of *Opisthotropis* together with seven or eight other generic names, thus bringing together a rather heterogeneous group of species. There are smooth and keeled forms; forms with maxillary teeth varying from 20 to 40, equal or "subequal" or having two or three much enlarged fanglike posterior teeth; groups with 19, 17, or 15 scalerows at midbody, groups with or without suboculars, etc. The one common character is the presence of a single prefrontal. Whether Günther's *atra* the type of the genus *Opisthotropis* is African as stated by Boulenger or is actually South Asian cannot be determined by us. We are recognizing Bourret's *Parahelicops* and placing this species in that genus rather than in *Opisthotropis*. It is significant that *Opisthotropis spenceri* M. Smith has been described from Thailand ("Muang Ngow, N. Siam") a

species having 17 smooth scalerows throughout, lacking the suboculars, and lacking the enlarged posterior maxillary teeth.

It is surprising that certain forms of both *Parahelicops* and *Opisthotropis* are nearly unicolored above and yellowish or whitish below. One suspects that this may be an adaptation to a stream habitat. However, but little is known of the ecology of these snakes.

SUBFAMILY HOMALOPSINAE

Enhydris plumbea (Boie)

Homalopsis plumbea Boie, 1827, p. 560 (type locality, Java).

Two specimens are at hand: EHT-HMS No. 31705 yg. (RE 3818) from Phu Phan (mt.), 550 m. elev., Sakon Nakhon (district and province), Thailand, June 28, 1954, Dr. Boonsong Lekagul and Robert E. Elbel, colls., and EHT-HMS No. 31706 (RE 541128), Kam (village), Khon Kaen (district and province), Nov. 28, 1954, collected by Robert E. Elbel.

These two have the following characteristics respectively: supralabials, 8-8, 8-8; infralabials, 10-10, 10-10; scale formula, 23, 19, 19, 15; 23, 19, 19, 13; ventrals, 127, 125; subcaudals, 39, 37; anals, 2, 2. Total length in mm., 220, 455; tail 31, 52.

No. 31706 contains 14 enlarged ovarian eggs.

Enhydris enhydris (Schneider)

Hydru: enhydris Schneider, *Historiae amphibiorum naturalis et literariae*, fasc. primus, 1799, pp. 245-246 (type locality, India orientalis, *fide* Russell).

One specimen, EHT-HMS No. 31759 (RE 541022) is at hand from near Kam (village), Khon Kaen (district and province), Thailand, collected Oct. 22, 1954, by Robert E. Elbel. It appears to be typical of the species. The following characters obtain: all scales smooth without pits; scale formula: 34, 21, 21, 21, 19; ventrals, 150; subcaudals, 47 + (tail broken); anal divided. Anterior chinshields shorter than second pair.

Dorsal scalerows nearly uniform brownish gray, the three outer scales at least partly without pigment. Ventrals outlined in brown; a median brown subcaudal line. The stomach contained eight small fish and parts of others. "Collected on road."

Homalopsis buccata (Linnaeus)

(Fig. 32)

Coluber buccatus Linnaeus, *Mus. Ad. Frid.*, 1754, p. 29, pl. 19, fig. 3; *Systema Naturae*, 10th Ed., 1758, p. 217 (type locality, India).

Homalopsis buccata Smith, *Jour. Nat. Hist. Soc. Siam*, vol. 1, 1914, p. 101; *idem ibid.*, vol. 1, no. 4, p. 162 (Bangnara, Patani); *ibid. idem*, vol. 1, p. 213

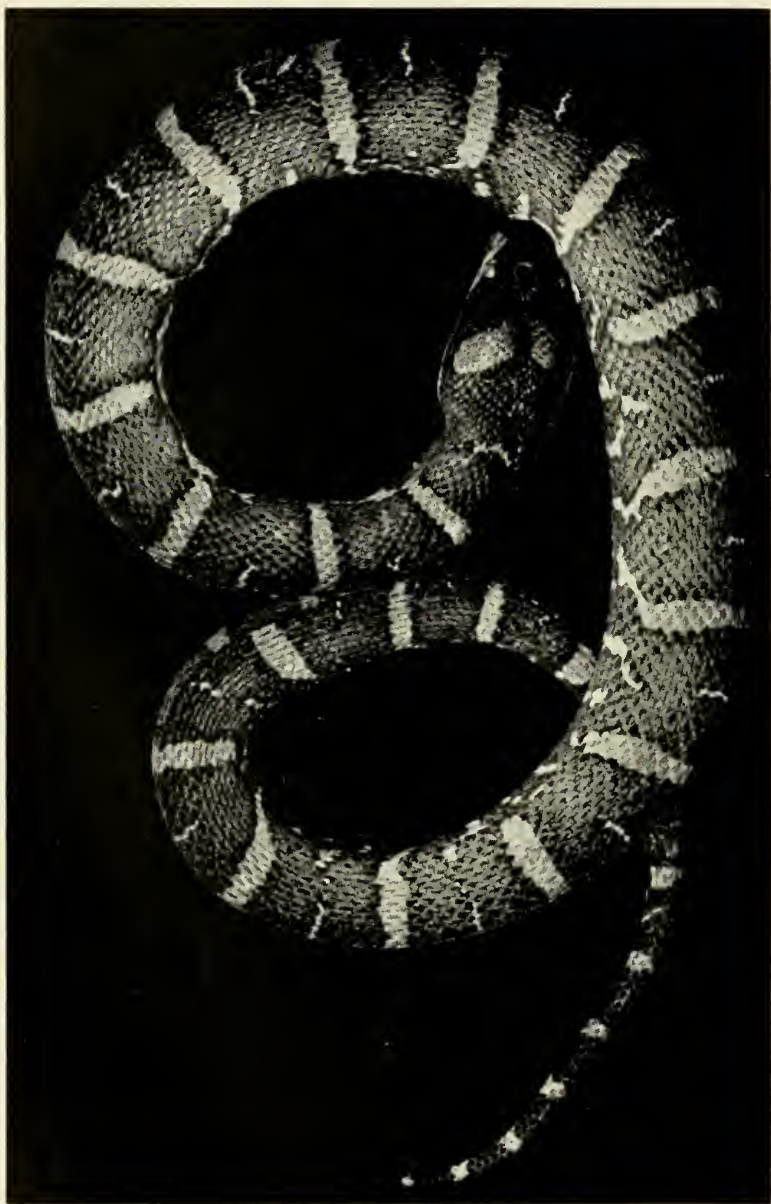


FIG. 32. *Homalopsis buccatus* (Linnaeus). EHT-HMS No. 31697, Phu Phan (mt.), 550 m., Sakon Nakhon (district and province), Thailand. Actual total length, 772 mm.

(listed); the fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese sub-region; Reptilia and Amphibia, vol. 3, Serpentes, pp. 390-392, fig. 123 (after Boulenger, 1890) (rivers, canals, ponds of Burma south of lat. 17°, Siam, Cambodia, Cochin-China, Malay Peninsula; Indonesia, usually found not far above tidal limits); Boulenger, A vertebrate fauna of the Malay Peninsula; Reptilia and Batrachia, 1912, pp. 162-163, fig. 50; Bourret, Les serpents de l'Indochine, tome 2, 1936, pp. 293-294, fig. 117 (listing of literature).

This widely distributed serpent is represented by four specimens: EHT-HMS Nos. 31694-31697 (RE 3818), all collected on Phu Phan (mt.), 550 m. elev., 104° 05'; 16° 55', Sakon Nakhon (district and province), Thailand, June 28, 1954, by Robert E. Elbel and Dr. Boonsong Lekagul. These vary in age and to some extent in color pattern. In No. 31695, the smallest specimen, (489 mm.), the body is brownish black on the back and sides, with 21 narrow (two or three scales wide) creamy-white transverse bands on body and 13 on tail. The bands on the back part of the body in some cases alternate with very narrow light lines which tend to divide the intervening dark blotches. An irregular cream line beginning at the mouth-angle runs back along the third and fourth scalerows for some distance, then becomes broken and some of the individual spots resulting are placed transversely on the venter. The venter is generally brownish black with many small rounded cream spots and anteriorly a few transverse bars, none completely crossing the venter.

A cream line from the angle of the mouth runs forward to below the eye to the nasal scale, while another begins at the same place, runs along the lower lip a short distance, then crosses the chin. From the middle part of the chin two cream lines run back onto the throat where they disappear. A pair of large rounded spots are present on the occiput.

In general this same detailed pattern is repeated in two other specimens, a male and female both larger than the described specimen. In a still larger specimen, No. 31696, the dorsal color is nearly brown and the transverse bands have become almost obsolete. The venter is brownish black showing small cream spots. The head markings are constant although dim in the largest specimen.

Measurements and scale data on Homalopsis buccata

Number	Total length	Tail	Chin scales	Ventrals	Anal	Sub-caudals	Scalerows
31695 ♂	489	114	11	157	2	84	48, 39, 27
31694 ♀	573	118	10	154	2 + 2	67	54, 39, 26
31696 ♂	782	185	8	160	2 + ½	82	53, 38, 27
31697 ♂	772	188	8	160	2	80	49, 39, 27

Malcolm Smith (1943) reports a Siamese specimen from "Eastern Siam, B. M. Coll." that has the whole lower part grey, thickly spotted with black. The largest known specimen measures 1310 mm., the tail being 285 mm. in length.

FAMILY ELAPIDAE

Bungarus candidus (Linnaeus)

Coluber candidus Linnaeus, Systema Naturae, 10th ed., 1758, p. 223 (type locality, India).

A specimen, KUMNH No. 31435 (RE 1063), was collected by the junior author Aug. 26, 1952, at Khorat (city and province), Thailand.

The following characters obtain: supralabials, 7-7, the third and fourth entering orbit; infralabials, 7-7; scale formula: 19, 15, 15, 15, the median row much enlarged; ventrals, 221; anal single; subcaudals, 42 + (tail incomplete). Total length, 1442; tail, 140 mm.

There are 23 light dorsal bars widening on the side, separated by 23 saddlelike black blotches, narrowing on the sides, reaching down and covering outer part of ventrals. The scales of the light areas have flecks or bars of dark color, the median row with two dark marks on each scale. A wide cream stripe follows the upper lip covering all or the greater part of all the labials. The top of the head is uniformly dark.

This is, we believe, the fifth specimen reported from Thailand.

Naja naja kaouthia Lesson

Naja kaouthia Lesson, in Ferrussac, Bull. Sci. Nat., vol. 25, 1831, p. 122 (type locality, Bengal).

Naja siamensis Laurenti, Specimen medicum, exhibens synopsis reptilium emendata . . . , 1768, p. 91 (type locality, Thailand), based on Seba, vol. 2, pl. 89, figs. 1-2.

There are three specimens of this cobra in the collections obtained by the junior author. These are KUMNH Nos. 40081-40082 (RE 2624) Khao Khat (mt.), approx. 500 m. elev., Paknampho (city), Nakhon Sawan (district and province), Thailand, June 4, 1953.

The following characters obtain in 31433: scale formula 27 (neck), 21, 14-15; ventrals, 161, subcaudals 34 +; anal single. Total length 987 mm.; tail, 115 mm. (tip incomplete). This is from the same locality as the other two.

FAMILY HYDROPHIIDAE

Enhydrina schistosa (Daudin)

Hydrophis schistosus Daudin, Histoire naturelle générale et particulière des reptiles, vol. 7 (an XI), 1803, p. 386 (type locality, "Coromandel").

A single young specimen of *E. schistosa* (KUMNH No. 40060) from Phet Buri, Thailand, was collected by Dr. Boonsong Lekagul.

The following scale characters obtain: rostral higher than wide, angulate above, the median lower part fitting into an indistinct notch in front part of lower jaw; nasals in contact, narrowed and angulate anteriorly, partly divided; one preocular, one postocular; prefrontals widened anteriorly, narrowed posteriorly, not in contact with labials; frontal small, narrower than a supraocular, angulate anteriorly and posteriorly, shorter than its distance from anterior end of nasals; eight supralabials, the four anterior enlarged, the fourth one entering orbit, four posterior ones small.

Temporals 1 + 1 + 2 + 4, the second touches the postocular; mental a very slender elongate scale nearly hidden in a groove; first supralabials narrow, much elongate, not in contact behind mental; two pairs of chinshields, the anterior largest in contact with three supralabials. Eight infralabials, the three or four posterior ones small.

Scale formula: 46 (head), 42, 47, 58, 35. Grayish white or cream with 34 brown spots on back and 4 on anterior part of tail (latter half of tail black). The specimen measures, total length, 325 mm.; tail, 38 mm.

Thalassophina viperina (Schmidt)

Thalassophis viperina Schmidt, Abh. Nat. Ver. Hamburg, Band 2, 1852, p. 79, pl. 3, (type locality, "Java").

The one specimen examined is BL No. 20063, Thailand (probably from the Gulf near Bangkok), collected by Dr. Boonsong Lekagul.

Lapemis hardwicki Gray

(Fig. 33)

Lapemis hardwicki Gray, Illustrations of Indian Zoology, vol. 2, 1834, pl. 87, fig. 2 (type locality, Penang); Smith, Monograph of the sea snakes (Hydrophiidae), London, Nov. 27, 1926, pp. 108-112, fig. 32, (Gulf of Siam).

A typical specimen of this widespread species (KUMNH No. 40063) from Phet Buri, Thailand, collected by Dr. Boonsong Lekagul, May, 1954, is in the collection. The total length is 646 mm.; tail, 66 mm.



FIG. 33. *Lapemis hardwicki* Gray. KUMNH No. 40063, Phet Buri (province), Thailand. Actual total length, 646 mm.

Hydrophis namillaris Daudin

(Fig. 34)

Hydrophis namillaris Daudin, *Historie naturelle générale et particulière des reptiles*, vol. 7, an XI=1803, p. 340 (based on Russel, vol. 1, p. 49, pl. 44 from Vizagapatam, India).

KUMNH No. 33517. We are associating with this species a specimen of sea-serpent from Bangphu (village), Bangkok, Thailand, collected by Dr. Boonsong Lekagul. The following characters

obtain: ten maxillary teeth following grooved fangs; 1 (2) pre-oculars, 1 postocular; supralabials, 7, second touches prefrontal on one side only; the fourth only enters orbit, last three small; infralabials, 10-10, three only touch the first chinshields, the second and third on one side separated from the lip by two or three intercalated

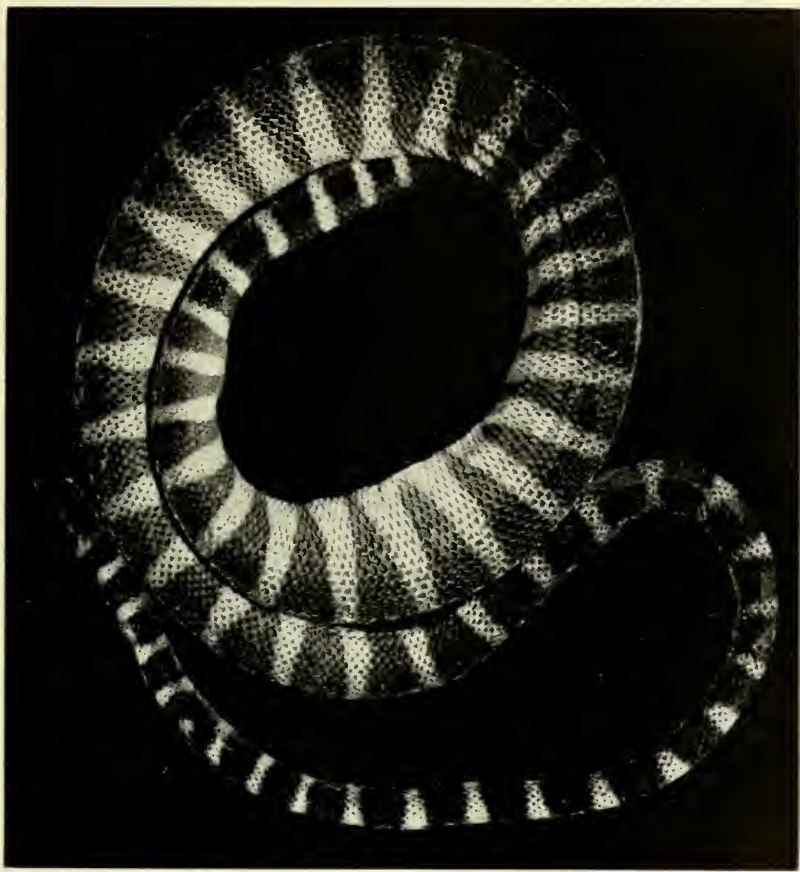


FIG. 34. *Hydrophis manillaris* Daudin. KUMNH No. 33517, Bangphu, Bangkok, Thailand. Actual total length, 655 mm.

small scales; posterior infralabials small. A single large anterior temporal followed by a still larger scale, and the latter touched by another enlarged temporal bordering the parietal. This last scale separated from its fellow by four small scales.

Scale formula, 36 (head), 33, 39, 32; ventrals, approximately * 325,

* Occasional small body scales are intercalated between ventrals making the count somewhat uncertain.

not double width of adjoining scales. Two preanals much enlarged, separated from each other by two and one half pairs of scales, the last pair extending somewhat behind them. A somewhat enlarged pair of postanal scales. Head small, scarcely wider than neck.

Head and neck about one-third times greatest diameter of body. Head black with a yellow streak on each side behind eye. Body blackish with 55 dark bands on body, and seven on flattened tail, wider dorsally, narrowing much on sides; except for the first eight, the white bands encircle the body, or occasionally fail to meet on venter by a very narrow margin. The dorsal and lateral scales of the light bands may have considerable pigment forming indefinite dark spots on the scales; most of the dorsal series of scales anteriorly have longer or shorter keels which more posteriorly become shortened into tubercles, the scales of the median dorsal row sometimes have two such tubercles, one following the other; ventrals usually with two lateral tubercles often indistinct.

The presence of a form of *mamillaris* in the Gulf of Siam is unexpected. There are some differences and with sufficient material a subspecific form might be recognized. The most significant differences are, only a single labial entering eye (the fourth); 33 scalerows around the neck; only a single postocular; only three scales touch the first small chinshields, the second pair distinguishable but not large. The head has a yellow streak on each side from nasal to eye and from eye to the first transverse white spot. There are two small scales bordering the lip between the anterior labials excluding the third labial on one side, and three small scales on the other side excluding both third and fourth from lip.

The species shows some similarity to *H. fasciatus atriceps* M. Smith and *holbrookei* Günther but the maxillary teeth are twice as numerous. It would appear that the maxillary teeth are less variable than other characters.

From *H. caerulea* it differs in a smaller number of teeth, smaller head and anterior body, a longer frontal, only *one* instead of two supralabials touching orbit, and a smaller number of scalerows on body.

The specimen is gravid, containing three very small embryos attached to large egg masses.

Hydrophis caeruleus (Shaw)

(Fig. 35)

Hydrus caeruleus Shaw, General Zoology, vol. 3, 1802, p. 561 (type locality, Indian Ocean).

Two young specimens, KUMNH Nos. 40061, 40062 from Phet Buri (province), Thailand, were collected by Dr. Boonsong Leka-

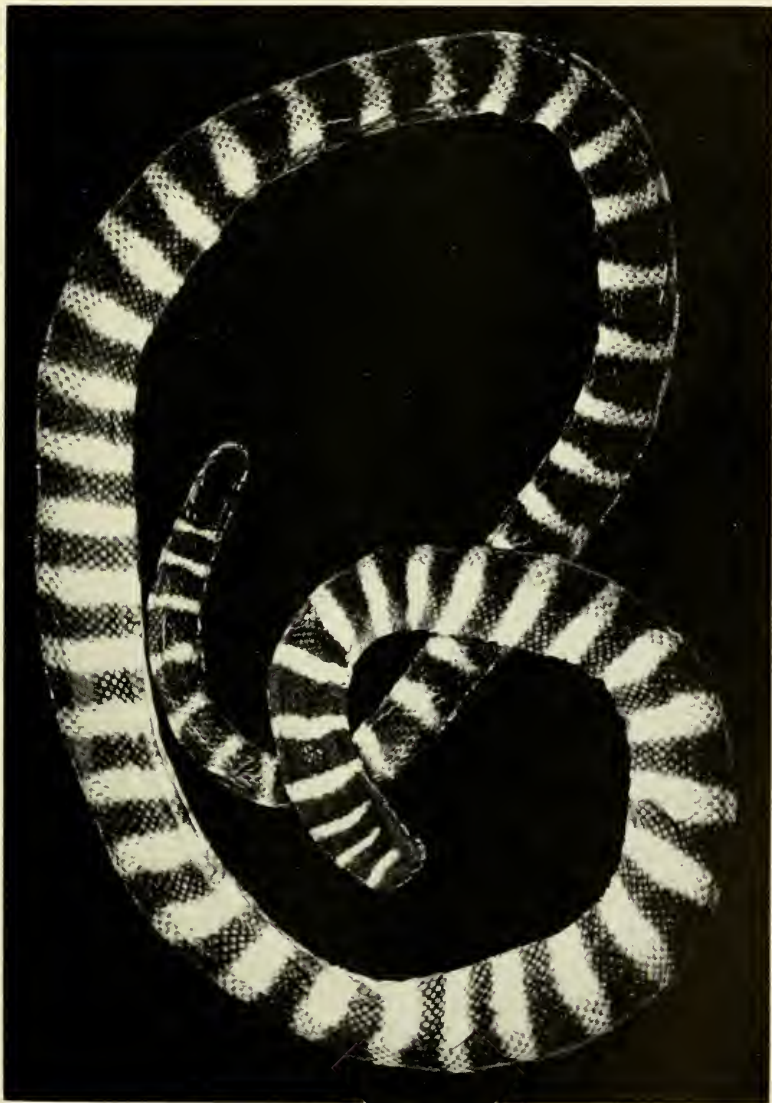


FIG. 35. *Hydrophis caeruleus* Shaw, KUMNH No. 40062, Phet Buri, Thailand. Actual total length, 537 mm.

gul. They have been assigned to *H. caerulescens* chiefly on the basis of the large number of teeth behind the poison fangs. In No. 40062 there are 14-16; in 40061 there are 14 teeth. The following characters obtain:

No. 40061: 1 preocular, 1 postocular, eight supralabials, the third and fourth enter orbit, the second touches prefrontal; the fifth labial is large and is possibly fused to the anterior temporal; last three labials small; infralabials seven, the first four small touching the anterior chinshields, last three small. Scale formula, 34 (neck)—42-35. Anal scales rather large, separated by three paired scales, the last pair almost completely behind them. Ventrals, 293; subcaudals, 410. Black bands on body and tail, 63, laterally tapering very slightly; those on tail connected below. Head black with some yellow lateral marks.

No. 40062 differs in some points. There are two postoculars on one side, the temporal is not fused to the labial, the anterior temporal contacts the eye at one point. There is a small scale on lip border between the third and fourth infralabials. There are 61 bands on body and tail; head without light marks; the light bands tend to be greatly narrowed, and interrupted ventrally; dorsally the white bands contain much dark pigment. Ventrals, 407; subcaudals, 36.

FAMILY CROTALIDAE

Agkistrodon rhodostoma (Boie)

Trigonocephalus rhodostoma Boie, Isis, 1827, p. 561 (type locality, Java).

One specimen, EHT-HMS No. 31718 (RE 3817) ♂, (bad state) is in the collection from Phu Phan (mt.), 550 m. elev. (104° 05'; 16° 55'), Sakon Nakhon (district and province), Thailand; June 28, 1954; Robert E. Elbel and Dr. Boonsong Lekagul, colls.

The following characters obtain: supralabials, 7-7; infralabials, 11-11, four touch the first chinshields; temporals, 2 + 1 + 2; two labials touch the single subocular; ventrals, 150; subcaudals, 53; scale formula, 19, 21, 21, 17.

KEY TO THAI SPECIES OF TRIMERESURUS

1. First labial fused partially or completely with the nasal 2
 First labial completely separated from the nasal scale 3
2. Upper head scales small subequal, tubercular or granular; supraoculars narrow (sometimes broken) separated by from twelve to fifteen scales; internasals two to three times size of adjoining scales, usually separated by a single scale; supralabials, 11-13, separated from the elongate subocular by from two to three rows of scales; scale formula, 25, (25, 27), (19, 21), strongly keeled. Usually

uniform purplish-brown or olive with spots; tail spotted with brown *Trimeresurus p. purpureomaculatus*

Upper head scales small, subimbricate; supraoculars narrow, not broken or divided, separated by from eight to twelve scales; internasals two to four times size of adjoining scales, usually in contact; 10-12 supralabials separated from large subocular by one or two rows of scales; scale formula, (21, 23), (21, 19), (15, 17). Green above, yellow or white below, males with a ventrolateral cream stripe, females with a row of light flecks on outer scalerow,

Trimeresurus albolabris

3. An elongate subocular present 4

Supraoculars divided; no white or cream line along outer scalerow; supraoculars divided transversely, separated by eight scales; internasals separated by a single scale; ten supralabials, a single series of scales between labials and the elongate subocular; temporal scales small with obtuse keels; scale formula, 19, 19, 15; ventrals, 152; subcaudals, 42, tail prehensile. Brownish gray with a series of brown spots and smaller ones on sides .. *Trimeresurus kanburiensis*

4. Supraoculars not divided transversely, usually their length equals twice their width, separated by from ten to thirteen subimbricate scales; internasals separated; temporals more or less strongly keeled; scale formula, 21 (23), 21, 15 (17). Green above, usually whitish below; a light stripe bordered below by orange or chocolate along flank and base of tail usually on first scalerow; a light post-ocular stripe. Hemipenes without spines .. *Trimeresurus popeorum*

Similar to preceding but hemipenes spinose .. *Trimeresurus stejnegeri*

Trimeresurus albolabris Gray

Trimeresurus albolabris Gray, Zool. Misc., p. 48, 1842 (type locality, "China"); Smith, Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese Sub-Region; Reptilia and Amphibia. Vol. III, Serpentes, Dec. 1943, pp. 523-525.

Six specimens are referred to this species despite considerable variation. They are EHT-HMS No. 31768 (RE 4259) from Ban Nong Wai (subvillage), approx. 1780 m. elev., Na Phung (village), Dan Sai (district), Loei (province), Thailand, Nov. 15, 1954; EHT-HMS No. 31769 (RE 541118), Ban Sang Kho (subvillage), Khok Phu (village), Sakon Nakhon (district), Sakon Nakhon (province), Thailand, Nov. 18, 1954; EHT-HMS No. 31770 (RE 4028), Ban Na Muang (subvillage), approx. 1780 m. elev., Na Haeo (village), Dan Sai (district), Loei (province), Thailand, Sept. 30, 1954; EHT-HMS No. 31801 (RE 5501), Phu Nam Lang (mt.) 1780 m., Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, 1955; KUMNH No. 40083 (RE 3217), Ban Muang Khai (subvillage), Tha Li (village), Tha Li (district), Loei (province), Thailand, Dec. 7, 1953. All specimens

collected by Robert E. Elbel except last, collected by Dr. Boonsong Lekagul and Robert E. Elbel.

A young specimen, EHT-HMS No. 31769 (RE 541118) shows the male markings clearly. It is nearly uniform greenish above (greenish blue with a large series of brown marks on each side of the body in preservative), the venter white growing olive on outer edges of ventrals. A cream-white line originating on preoculars passes below the eye and over temporals covering most of two whole rows of temporals, then, crossing mouth angle, it continues along the outer scalerow covering more than half of each scale; on the tail it passes onto the outer part of the much widened subcaudals. The prehensile tail is more or less spotted with brown. Chin and to some extent throat, white; rostral and two first supralabials partly white.

The following scale characters obtain: supraoculars large, their length three times their width, separated from each other by nine scalerows, the scales flat, smooth, imbricate, the temporals not or but very indistinctly keeled. Internasals large, in contact, three to four times size of the adjoining canthal; supralabials, 11-12, first fused to nasal; long curved subocular; two postoculars; third supralabial touches the subocular; fourth separated from it by one scalerow, succeeding ones by two rows; infralabials, 12-14; two pairs of chinshields, the second small, in contact, separated from ventrals by four pairs of scales; scale formula: 46 (head), 21, 21, 15; scales not discernibly keeled; ventrals, 163; anal single, subcaudals, 73 + 1; total length, 251 mm.; tail, 45 mm.

The coloration of this specimen is quite different from that reported by other workers for the species. The specimen is very young and this coloration possibly is lost in the adult. The absence of keels on the scales is possibly owing to the youth of the specimen.

No. 31768 ♀. The following characters obtain: *internasals in contact*, three to four times as large as the two canthals; supraoculars four times as long as wide, separated by ten or eleven smooth, subimbricate scalerows; *three postoculars*, one long subocular; the fourth and fifth scales separated from it by one scale; rostral one and two-thirds times as wide as high; two pairs of chinshields, followed by four paired scales; infralabials, 12-11; ventrals, 157; anal single; subcaudals, 75 + 1; scale formula, 44 head, 23, 21, 15, *scales completely smooth*; no ventrolateral line and no line behind or under eye; whitish on chin; a row of light flecks on outer scalerow. Tail uniformly colored.

No. 31770 ♀. Internasals one and one-third times as long as wide, separated by two scales, one following other; two canthals less than half size of internasals; loreal present, reaching or just failing to reach canthal edge; 11-10 supralabials, *the first more than half fused with nasal*, the third touching subocular, fourth separated by one scale, fifth by two; two postoculars; one long subocular widened anteriorly; supraoculars four times as long as wide, separated by nine or ten small subimbricate scales; posterior temporals definitely ridged or keeled; *one pair of chinshields followed by six paired scales*, none separated by small scales; scale formula, 44 (head), 21 (22), 21, 15; ventrals, 167; subcaudals, 58 + 1. A row of cream flecks on outer scalerow. *Tail brown spotted.*

No. 40083. *Internasals rectangular*, about two and one-half times longer than wide, *separated by a single scale*; supraoculars about two and one-half times as long as wide, separated by 11-12 scales, not keeled but somewhat thickened, sometimes moundlike; supralabials, 12-12, *first completely fused to nasal*, third touches the subocular; other labials separated from it by two rows of scales; infralabials, 14-14; *two pairs of chinshields*, followed by four paired scales none separated by small scales; two postoculars; scale formula, 48 (head), 21, 21, 15. The ten to fifteen dorsal scalerows well keeled; ventrals, 163; subcaudals, 52 + 1.

Color (in preservative): uniform bluish-black, grayish on tail; venter bluish or bluish black, the posterior edges of the ventrals light; a row of light flecks on outer scalerow; tip of lower jaw black; light areas on chin and beginning of throat. *Tail grayish, not brown spotted.*

When skin is distended there appears to be transverse rows of light flecks, the light color being on skin between scales; these separated by similar dark areas. This occurs more or less distinctly in all the specimens (in 31769 the whole "light" area is brown).

Trimeresurus popeorum Smith

(Fig. 36)

Trimeresurus popeorum Smith, Jour. Bombay Nat. Hist. Soc., vol. 39, p. 730 (original spelling *popeiorum*, a clerical error, was corrected by the author) (restricted type locality, Khasi Hills, Assam).

Two specimens are referred to this species. They are EHT-HMS Nos. 31799 (RE 5503) and 31800 (RE 5620) from Phu Nam Lang (mt.), 1780 m. Ban Khok (subvillage), Na Phung (village), Dan Sai (district), Loei (province), Thailand, June 2, and June 10, 1955, respectively. Robert E. Elbel, collector.

The second specimen, 31800, has the following characters: rostral angular, slightly wider than high, narrower than mental; two loreals superimposed; eye relatively large, the length of snout a little less than twice its greatest diameter; internasals large, double the size of two enlarged contiguous canthals, but three to four times larger than other scales adjoining, separated from each other by one

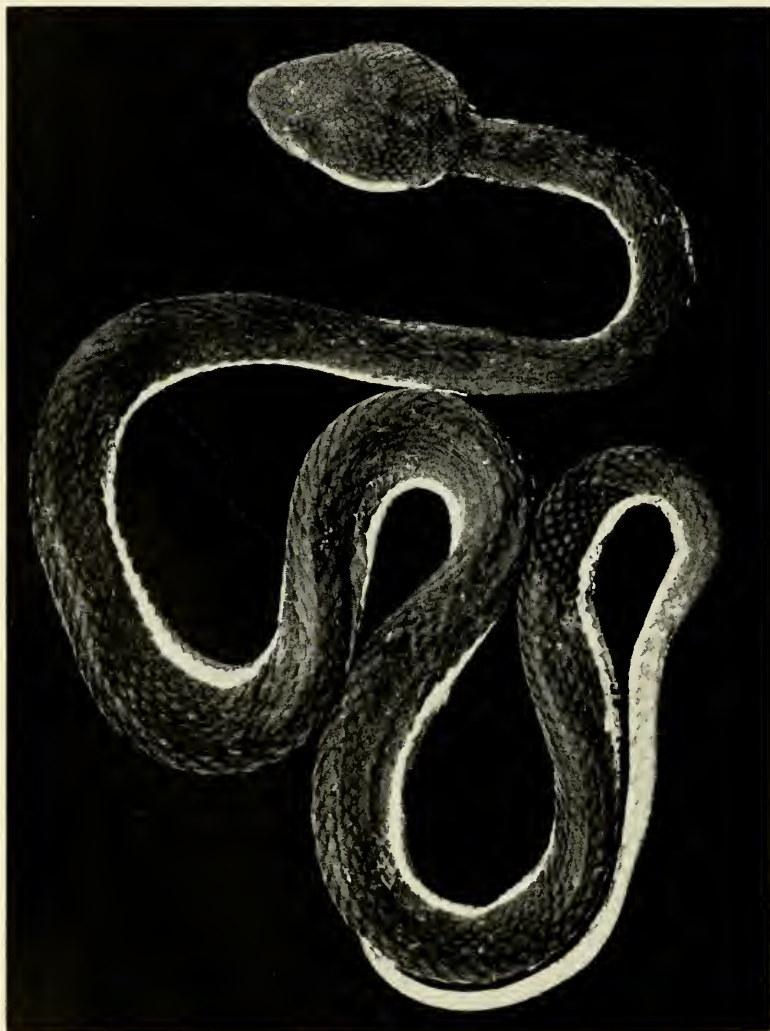


FIG. 36. *Trimeresurus popeorum* M. Smith. EHT-HMS No. 31800, Phu Nam Lang (mt.), 1780 m. elev., Ban Khok, Na Phung, Dan Sai, Loei (province), Thailand. Actual total length, 412 mm.

elongate scale; supralabials, 10-9, the first completely free from nasal, the second high forming anterior border of the pit, the third labial largest separated from the elongate subocular by one scale, the fourth labial separated from same by one (or two) scales; infralabials, 12-12, three touch chinshields; only one differentiated pair of chinshields, followed by five pairs of scales preceding the first ventral, the two anterior pairs separated each by a pair of small scales; supraoculars three to four times as long as wide separated from each other by 12-13 irregular rows of smooth subimbricate scales; temporals bordering labials largest. Scale formula, 45, head, 21, 21, 15; the dorsal 15 series vaguely keeled; posterior temporals with short posterior elevations or keels; subocular narrow, elongate, curving; two postoculars. Ventrals, 167, anal single, subcaudals, 64 + 1. Tail prehensile, slender, and practically the same diameter for much of its length. Total length, 412 mm.; tail 69 mm.

Dorsally nearly uniform green (dark blackish in preservative); a light ventrolateral line, cream above, orange along its lower edge, covering all of the outer scalerow, the lower two fifths of second row, and the extreme outer edge of ventrals; on the tail only part of the outer row is involved, the stripe covering also outer part of subcaudals. Tail flecked and spotted with brown and black, except terminal part which is uniform light brown. Beginning back of eye a cream line bordered by orange above runs diagonally back, crosses mouth-angle and is continuous with the ventrolateral stripe.

The second specimen is a young female. It agrees in general with the characters given. The following characters obtain: supraoculars three times as long as wide separated by 10-12 scales; length of snout not double eye diameter; internasals separated by two scales (abnormal); two loreals small, superimposed; supralabials, 10-10, first separated from nasal, third separated from eye by one scalerow, the fourth and succeeding labials by two rows; infralabials, 12-12; one pair of chinshields, followed by 5 pairs of scales, the first two separated by small scales. Scale formula, 48, 21, 21, 15; ventrals, 165; anal single; subcaudals, 57 + 1.

Head and body uniform bluish black except for a narrow bluish white line confined almost entirely to middle of the outer scalerow; on tail the outer edges of the subcaudals are somewhat involved. Total length, 285 mm.; tail, 44 mm.

Remarks: Malcolm Smith founded the name, *T. popeorum* on *T. gramineus* (Shaw) Pope and Pope. No type locality was mentioned by Smith.

The material treated by Pope and Pope under *T. gramineus* had a range from "Upper Burma southward into the Malay Archipelago". The exact localities were Darjeeling, Bengal; Mergui, Tenasserim; Prov. Wellesley, Malay Peninsula; Pinang, Malay Peninsula; "Sungei Kumbang, Korinchi", Sumatra; Lao Mts. Cochin-China; Saiap, Kina Balu, Borneo.

A detailed description of one specimen, (British Museum Register No. 72.4.17.137, Khasi Hills, Assam, Jerdon collector), is given by Pope and Pope. We propose to designate this specimen as the holotype of *T. popeorum*, and to restrict the type locality to Khasi Hills, Assam.

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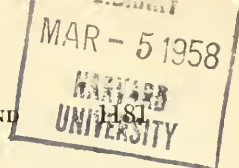
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Report on a Collection of Amphibians and Reptiles from Harbel, Republic of Liberia

BY

EDWARD H. TAYLOR * and DORA WEYER **

The collection of Liberian reptiles and amphibians reported herein has been brought together by Mrs. Dora Weyer, the junior author, while residing at The Firestone Rubber Plantations at Harbel, Liberia. Her husband, Dr. Albert E. Weyer, director of sanitation, has assisted her to some extent in this work.

The collection contains a number of rarities and certain species are regarded as new. Field notes appearing in quotation marks are those of the junior author, sent with the collection.

"All of these specimens come from the main Firestone plantation save one from the Cavalla plantation—very similar ecologically but southeast of Harbel on the Cavalla River.

"Ecologically Harbel is in the heaviest rain-forest in Africa. The soil is a gravelly laterite, with many outcroppings of rocks. The large Du and Farmington rivers curve back and forth through the area and there is a multitude of small rivers and creeks tributary to them fed by water from innumerable swamps. This is an area of low hills rising from the coastal sand plain which edges the plantation seaward and lying between each hill and the next is usually a swamp! In fact, the survey map shows 25 percent of the entire area is swamp.

"Lastly, of interest from an ecological viewpoint, with the exception of certain experimental plots, the river edges, and the cutover swamp lands, the area is covered with dense rubber forest. In the old rubber forest with trees reaching 75 to 90 feet in height, and where most of the collecting was done, the ground cover is pretty

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well limited to grass and ferns which is cut over three or four times a year to keep it low. In the young rubber the ground is densely covered with a kudzulike legume used here for a cover crop; this dies out once the trees get big enough to shade it.

"Ten miles beyond the plantation borders at Kakala the annual rainfall is only 80 inches while farther on at Ganta it drops to 60 inches. Here at Harbel the annual rainfall runs from 150 to 200 inches.

"While there are no extensive serpent cults in Liberia such as have been reported elsewhere in Africa, there are 'snake charmers' or persons who 'play' with snakes.

"The tribes near Harbel have their 'snake men' who handle or 'play' with the snakes. Incidentally, they do not necessarily remove the venom from the poisonous snakes with which they play. I had assumed that they did remove the poison. Recently two 'snake men' were brought into the hospital dead, and the physician, my husband, questioned the people who brought them in. They came from a village near the plantation—a Kepelle village—and both of the deceased were full-fledged initiates. Presumably each 'snake-man' keeps his own poisonous snake either in a basket, in his hut, or loose in the 'bush' behind his hut. When the time comes that he wishes to show his prowess, or more likely force tribute from someone, he goes to the bush and calls his snake. When the snake comes to him he is supposed to ask it whether it wishes to 'play' in the village. Only if the snake agrees may he handle it safely before the people—and this is not done often.

"However in the case in question, the two men together were playing with the snake, a cobra, in the village when suddenly it bit one. The other man instantly took it from the hand of the bitten man, and the snake bit him also. Both died after a short time.

"When questioned by my husband the witnesses answered that they did not think the second man realized that the snake had actually bitten his associate, but had thought that the snake was simply playing, and he merely wanted to handle the snake himself.

"When asked why they thought the men's medicine had not worked they carefully explained two possibilities:

"(1) The snake may not have 'agreed' to play in the village and they took it in spite of this, or (2) the men may not have fully performed the initial rites or may have broken the prescribed taboos, one of which is that they must not have had sexual intercourse for three days previously.

"All this of course is a deadly serious matter to these people. An examination of the snake showed that it retained the fangs. The poison sac was intact and still contained some poison."

LIST* OF AMPHIBIANS AND REPTILES KNOWN TO OCCUR IN THE REPUBLIC OF LIBERIA

AMPHIBIA

GYMNOPIHIONIANs

Geotrypes seraphini occidentalis Parker

**Geotrypes angeli* Parker

SALIENTIA

**Xenopus tropicalis* Gray

Bufo regularis regularis Reuss

Bufo regularis maculatus Hallowell

Bufo togoensis Ahl

Bufo camerunensis camerunensis Parker

Hemisus marmoratus (Peters)

Rana albolabris albolabris Hallowell

Rana albolabris parkeriana Loveridge

Rana mascareniensis mascareniensis Duméril and Bibron

Rana bibroni Hallowell

Rana occipitalis Günther

Rana oxyrhynchus oxyrhynchus Smith

Rana oxyrhynchus gribinguiensis Angel

Rana longirostris Peters

**Rana maccarthyensis* Andersson

Rana crassipes alleni (Barbour and Loveridge)

Rana subsigillata A. Duméril

Phrynobatrachus giorgii De Witte

Phrynobatrachus perpalmatus Boulenger

Phrynobatrachus francisci Boulenger

Phrynobatrachus natalensis (Smith)

Phrynobatrachus latifrons Ahl

Phrynobatrachus plicatus (Günther)

Phrynobatrachus alleni Parker

Phrynobatrachus ogoensis brongersmai Parker

Phrynobatrachus liberiensis Barbour and Loveridge

Arthroleptis adolfi-friederici Nieden

Arthroleptis calcaratus (Peters)

Arthroleptis poecilonotus Peters

Arthroleptis taeniatus Boulenger

Arthroleptis werneri Nieden

Arthroleptis guttersus Chabanaud

Cardioglossa decorata Barbour and Loveridge

Cardioglossa liberiensis Barbour and Loveridge

Leptopelis viridis (Günther)

Leptopelis bequaerti (Loveridge)

Leptopelis tessmanni Nieden

* Species occurring in the collection at hand are preceded by an asterisk.

Peptopelis bocagii (Boulenger)
Hylambates hyloides Boulenger
Hylambates cochranae Loveridge
Hylambates leonardi Boulenger
Megalixalus immaculatus Boulenger
Megalixalus fulvovittatus Cope
Megalixalus fornasinii (Bianconi)
Megalixalus platyceps Boulenger
Hyperolius concolor (Hallowell)
Hyperolius puncticulatus Pfeffer
Hyperolius platyceps Boulenger
Hyperolius festivus Barbour and Loveridge
Hyperolius pleurotaenides (Boulenger)
Hyperolius ocellatus Günther
Hyperolius fuscigula Bocage
Hyperolius fusciventris Peters
Hyperolius marmoratus Rapp
Hyperolius picturatus Peters
Hyperolius admetzi Ahl

REPTILES

CROCODILES

Crocodylus niloticus Laurenti **
Crocodylus cataphractus Cuvier
Osteolaemus tetraspis Cope

TURTLES

Eretmochelys imbricata imbricata (Linnaeus)
Chelonia mydas mydas (Linnaeus)
Dermochelys coriacea coriacea (Linnaeus)
Lepidochelys olivacea olivacea (Eschscholtz)
Kinixys homeana Bell
 **Kinixys erosa* (Schweigger)
Pelusios adansonii (Schweigger)
Pelusios † *subniger* (Lacépède)
Amyda triunguis Forskål

AMPHISBAENIANS

Amphisbaena liberiensis Boulenger
Amphisbaena cynisca leucura Duméril and Bibron

SAURIANS

Hemidactylus mabouia (Moreau de Jonnes)
Hemidactylus muriceus Peters
Hemidactylus fasciatus Gray
Lygodactylus thomensis Peters
Lygodactylus gutturalis (Bocage)
 **Agama agama africana* (Hallowell)
Varanus (Polydaedalus) *niloticus niloticus* (Linnaeus)

** The name of an author associated with a scientific name may be regarded as being in the genitive case; hence it would appear that *Laurenti* is the proper form if one inflects the name as is done in the title of certain books.

† *Pelusios derbianus* Gray and *Pelusios nigricans castaneus* Hewitt are placed in the synonymy of *P. subniger* by Mertens and Wermuth 1955. These names have been recognized previously as representing distinct species.

- **Lacerta echinata echinata* Cope
- **Mabuya maculilabris maculilabris* Gray
- **Mabuya blandingii* Hallowell
- Mabuya bensoni* (Peters)
- Riopa durum durum* Cope
- **Riopa fernandi* (Burton)

CHAMAELEONS

- **Chamaeleon senegalensis* Daudin
- Chamaeleon gracilis gracilis* Hallowell

SERPENTS

- **Typhlops leprosus* sp. nov.
- **Typhlops punctatus punctatus* Leach
- Typhlops manni* Loveridge
- Python sebae* Gmelin
- **Calabaria reinhardti* (Schlegel)
- **Neusterophis variegatus* (Peters)
- **Natrix anoscopus anoscopus* (Cope)
- **Natrix firestonei* sp. nov.
- Lycophidion fasciatum* Günther
- **Bothrophthalmus lineatus lineatus* Peters
- Boaedon olivaceus* (Duméril)
- **Boaedon lineatus virgatus* (Hallowell)
- **Boaedon lineatus lineatus* Duméril, Bibron, and Duméril
- **Hormonotus modestus* Duméril, Bibron, and Duméril
- Chlorophis irregularis* (Leach)
- **Chlorophis heterodermis* (Hallowell)
- Phylothamnus nitidus* (Günther)
- Gastropyxis smaragdina* (Schlegel)
- Mehelya guirali* (Mocquard)
- **Mehelya poensis* (Smith)
- Coronella coronata* (Schlegel)
- Hapsidophrys lineata* Fischer
- Grayia smythii* (Leach)
- Rhamnophis aethiopissa aethiopissa* Günther
- Thrasops flavigularis* (Hallowell)
- Dasypeltis scaber* Linnaeus
- Dasypeltis macrops* Boulenger
- Crotaphopeltis hotamboeia hotamboeia* Laurenti
- Crotaphopeltis duchesnii guineensis* (Chabanand)
- Boiga pulverulenta* (Fischer)
- **Boiga blandingii* (Hallowell)
- **Psammophis sibilans phillipsi* Hallowell
- **Thelotornis kirtlandii kirtlandii* (Hallowell)
- Miodon acanthias* (Reinhardt)
- Apparallactus lineatus* Peters
- **Apparallactus modestus* (Günther)
- Dendroaspis viridis* (Hallowell)
- Dendroaspis jamesonii* (Traill)
- Naja nigricollis* Reinhardt
- Naja goeldii* Boulenger

- **Naja melanoleuca* Hallowell
 - **Atractaspis corpulenta* (Hallowell)
Atractaspis irregularis Reinhardt
 - **Causus rhombeatus* (Lichtenstein)
Causus lichtensteini (Jan)
 - **Bitis gabonica* Duméril, Bibron, and Duméril
 - **Bitis nasicornis* (Shaw)
Atheris chlorechis (Schlegel)
-

REPORT ON THE COLLECTION

Geotrypetes angeli Parker

Geotrypetes angeli Parker, Zool. Meded. Leiden, vol. 19, 1936, pp. 100-101 (type locality Labé, French Guinea, Africa); Loveridge, Proc. New England Zool. Club. vol. 17, May 20, 1938, p. 65, (Sanoquelle, near Santa, Liberia).

Although this species is described in Parker's paper on "The Amphibians from Liberia and the Gold Coast," it would seem that it is known from neither territory. It is presumed that Loveridge's record represents the first report of the species for Liberia.

Two specimens are at hand, EHT-HMS Nos. 31927, 31928 from Harbel, Liberia. They yield the following data: (the heads of both, and the tail of one, have been somewhat injured. The count here given of the grooves and teeth, if not actual, are very close to the actual number.)

No. 31927. Eye distinct; snout elongate, projecting considerably beyond lower jaw; distance between eye and mouth contained nearly three times in distance between eye and nostril; tentacle below nostril nearly midway between nostril and lip; a total of 31 maxillary-premaxillary teeth, the posterior smallest; about 34 vomeropalatine teeth, the posterior much the smallest; dentary series 28; splenial series 18. In No. 31928 the maxillary-premaxillary teeth are 29; vomeropalatine 34; dentary series 24, splenial series 20.

The general color (in preservative) is lavender-purplish to violet. Most of the grooves are grayish white, and the head is somewhat lighter, perhaps somewhat olive in life.

Measurements in mm. (of 31927, 31928 respectively): Total length 279, 202; head length, 12.2, 9.2; distance between eyes, 4, 3.3; eye to tip of snout, 4.15, 4; eye to nostril 3.5, 3; eye to lip, 1.25, 1.05; greatest diameter of body, 10, 5.

The hidden scales begin somewhere on the anterior two fifths of the body. At first they are minute and usually to be discovered at the upper end of the primary grooves. At the beginning of the secondary grooves they are of larger size and cover much of the space

between the primary and secondary grooves; the scales anteriorly are much longer than wide, farther back they may be nearly as wide as long. The greatest measurement is always transverse.

Xenopus tropicalis (Gray)

Silurana tropicalis Gray, Ann. Mag. Nat. Hist., ser. 1, vol. 14, 1864, p. 315; and Proc. Zool. Soc. London, 1864, p. 458. (type locality, Lagos).

Xenopus tropicalis Parker, Proc. Zool. Soc. London, April 16, 1936, p. 156 (distinguishing characters); Loveridge, Proc. U. S. Nat. Mus., vol. 91, 1941, p. 124, (Gibi and Bromley, Liberia).

A young specimen, EHT-HMS No. 31948 (snout to vent 29 mm.) is from Harbel, Liberia. The head is much more depressed than the figures presented by Parker (*loc. cit.*) show but this may be due to the youth of the specimen.

Rana maccarthyensis Andersson

Rana maccarthyensis Andersson, Arkiv. Zool., vol. 29A, no. 16, 1937, p. 9, figs. 3-4 (type locality, McCarthy Island, Gambia); Loveridge, Proc. U. S. Nat. Mus. vol. 91, 1941, p. 136 (specimens from Gibi and Bellyella, Liberia).

One specimen, EHT-HMS No. 31947, Harbel, Liberia. Loveridge had certain specimens in which the legs were reported as being longer than those in the type. In this specimen the tibiotarsal articulation reaches the nostril. Both inner and outer metatarsal tubercles are present, the latter connected by a row of low tubercles with the posterior subarticular tubercle of the fourth toe; vocal sacs external, opening through a slit on each side of the throat; the vocal sacs are black and the slits are parallel to each other extending posteriorly toward the "lower insertion of forearm"; three or four longitudinal folds on each side of dorsum, the longest extending more than half the length of body. The tympanum is longer than high, its greatest diameter equals four fifths or more of the length of the eye-opening. Three large palmar tubercles, the outer elongate; the posterior subarticular tubercles of fingers very large.

There are two longitudinal series of white dots more or less connected on front and back of thigh, and a broad median light stripe present.

Kinixys erosa (Schweigger)

Testudo erosa Schweigger, Prodr. Monog. Chelon., 1814, p. 52.

Kinixys erosa Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 39, 1919, pp. 403-406, Map-3, pl. XI, fig. 1. (bibliography).

A single specimen EHT-HMS No. 31938 is from Harbel, Liberia. The specimen is young, the greatest over-all length of the carapace being only 145 mm. While the hinge of the carapace is scarcely evident to the eye, the carapace is closely pressed against the plas-

tron behind. The denticulation is strongly marked along the flaring anterior edge of the carapace, some scutes bearing two or more denticulate projections. The lateral marginals have single serrations, the posterior ones have a scalloped appearance.

There are four claws on the hind foot, five on the fore foot.

Agama agama africana (Hallowell)

Tropidolepis Africanus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1844, p. 171 (type locality, Liberia).

Agama agama africana Loveridge, Proc. U. S. Nat. Mus., vol. 91, no. 3128, 1941, p. 116 (Bellyella, Bendaja).

A single young and two adult male specimens, EHT-HMS No. 31926, 31943, and 31944, from Harbel, Liberia, are in the collection. The number of preanal pores ("callose preanal scales") situated on the border of the vent are 12, 12, and 11, respectively.

Lacerta echinata echinata Cope

Lacerta (Zootaca) echinata Cope, Proc. Acad. Nat. Sci. Philadelphia, 1862, pp. 189-190 (type locality West Africa [probably Liberia, *vide* Loveridge *loc. cit.*]).

Lacerta echinata Barbour and Loveridge, in Strong Contr. Dept. Trop. Med. and Inst. Trop. Biol. Medicine No. 5, vol. 2, 1930, p. 776. (Plantation 3, Du River).

Lacerta echinata echinata Loveridge, Proc. U. S. Nat. Museum, vol. 91, No. 3128, 1941, pp. 116-117 (Harbel).

A single specimen, EHT-HMS No. 31924, has the following characters:

Part of rostral visible above as long as the median suture between the anterior nasals; frontonasal longer than wide, touching the anterior loreal laterally; prefrontals longer than wide, their common suture less than half their greatest length, touching both loreals, the anterior supraocular, and the anterior supraciliary; frontal approximately one-third longer than wide; frontoparietals nearly as large as prefrontals but with a longer median suture, touching two supraoculars; parietals longer than wide, each with an irregular longitudinal ridge or keel the outer posterior part of the scales depressed; a well-defined postinterparietal; nostril surrounded by rostral (narrowly), first labial, posterior and anterior nasals; five (four) supralabials precede the large subocular; latter followed by a large,—and one or two very small, supralabial scales; seven or eight infra-labials; a large mental scale with a labial border much greater than that of the rostral; three pairs of much enlarged chinshields the anterior pair forming a median suture, second pair narrowly separated anteriorly, third pair separated by ten or more rows of small

scales; third chinshield followed behind by two scales. Three supraoculars, the third one-third or one-fourth times size of the first and second; a row of 10 supraciliaries, the first and last largest; about 12 rows of keeled temporal scales in preauricular area; tympanum oval, much higher than wide; scales on neck and body small, strongly keeled, the keels in nuchal region parallel to body, those on side of body running up and back, the keels diagonally placed on the individual scales.

Venter covered by six longitudinal rows of large scutes in about 32 transverse rows. The median rows are slightly the smallest, the rows adjoining these largest, the outer series somewhat intermediate, and in turn bordered by a row of scales somewhat larger than the lateral body scales; scales on underside of neck small with a distinct collar of larger scales, which may be preceded by one or two enlarged scales. Anal scale large, bordered on sides and posteriorly by two rows of scales; 10-11 femoral pores.

Tail above and below with sharply keeled scales, those near the base—between the tenth and twentieth whorls—with longer mucrones extending from the posterior part of the keels; a row of five or six enlarged keeled scales on outer face of upper arm more or less continuous with a series of ten on front face of forearm; a similar series on front face of femur and on tibia, the series being largely ventral; other scales on limbs variable in size; subdigital scales not strongly keeled.

Color (in preservative): Top and sides of head nearly uniform blackish; body generally dark grayish-black with transverse gray-lines crossing neck and extending down to near the ventral surface; on body the transverse markings are less distinct, rarely continuous, often consisting of four or more tiny gray spots; tail dark with extremely narrow vertical lines of white, the upper ones often alternating with those low on sides of the tail; chin and large scutes of belly lighter, but with considerable pigment, becoming blackish on the two outer rows of scutes.

Measurements in mm.: Snout to vent, 76; tail 203; total length, 279.

Remarks: The original description by Cope varies somewhat from the description given here but this may be due, at least in part, to a different terminology. The color, as given by Cope is: "Above bluish-green with about fifteen blackish cross bands; those upon the nape and rump are narrow, the others broad, dark bordered. Beneath yellowish. Head shaded with yellowish."

Whether this pattern is essentially different or has been modified in preservation cannot be stated at this time.

We have followed Loveridge in using the trinomial, although there may be some doubt that *Lacerta langi* Schmidt is actually a subspecies of this form.

Mabuya blandingii (Hallowell)

Euprepis Blandingii Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1844, p. 58 (type locality, Liberia).

Mabouia raddonii Gray, Catalogue of the specimens of lizards in the collection of the British Museum, 1845, p. 11 (type locality, West Africa); Boulenger, Catalogue of the lizards in the British Museum, 2nd ed., vol. 3, pp. 165-166, pl. 10, fig. 1 (includes *blandingii* as a synonym).

Mabuya blandingii Loveridge, Proc. U. S. Nat. Mus. vol. 91, no. 3128, 1941, p. 117. (Gibi, Bromley, Bendaja, Harbel).

There are several mabuyas in the collection (EHT-HMS Nos. 31930, 31931, 31934, 31937) which are in bad condition (having been dried). It is thus practically impossible to ascertain relative lengths of limbs or to discern clearly original markings and coloration. It would appear that more than a single species is indicated. Some of these certainly belong to *blandingii*, however, all are included here. Loveridge (*loc. cit.*) has indicated that he believes the variation is considerable, and places all twelve specimens, examined by him, in this species.

All of our specimens have a lateral white line. Two are characterized by having the frontal touching only the two anterior supraoculars, with the prefrontals widely separated by the junction of the frontal and the frontonasal. There are 30 scalerows about the body. The body scales are 3-keeled, or the outer parts of the scale may have also a tubercle. The scales in the median nuchal region may have four normal keels and the two nuchal scales are not or but dimly keeled. Two other specimens have the frontal touching only the second and third supraoculars, the body scales are 3-keeled, but the nuchal scales may have five or seven keels and the nuchals 12 or 13 distinct keels. There are 30 scalerows about the body. Another specimen has the frontal touching the first, second, and third supraoculars, and there are 30 scalerows present.

Mabuya maculilabris maculilabris (Gray)

Euprepis maculilabris Gray, Catalogue of the specimens of lizards in the collection of the British Museum. 1845, p. 114.

Mabuia maculilabris Boulenger, Catalogue of the lizards in the British museum (Natural History). 2nd ed., vol. 3, 1887, pp. 164-165, pl. 9, fig. 2.

EHT-HMS No. 31933 in the collection from Harbel, Liberia, has the following characters: internasals injured, presumably minutely

separated; frontonasal broader than long; prefrontals forming a median suture, in contact with first and second supraoculars; frontal slightly longer than its distance from the tip of the snout, shorter than the median combined length of parietals; two frontoparietals; an interparietal enclosed by the parietals, which are wider than long; a pair of nuchals (nearly smooth, only back edge suggests keeling); nostril almost directly above suture between rostral and first labial; a distinct postnasal, in contact with first labial (or also very narrowly with second on one side); two loreals the posterior largest, the anterior barely touching a labial on one side; two pre-suboculars; a transparent eyelid disc; six or seven supraciliaries; four supraoculars, frontal touching only second and third; seven supralabials, the subocular supralabial, the fifth, nearly double width of two preceding; eight infralabials; two primary, three secondary temporals; four postoculars.

Arms and legs well developed, the toes reaching the elbow of adpressed arm; subdigital lamellae without distinct keels or spines; 33 scalerows around neck; 32 around middle of body, most of the body scales having five distinct keels, some of those on neck behind parietals with seven or eight; ear bordered anteriorly by four irregular denticulations; 12 ventral rows of scales smooth; tail regenerated, with 85 subcaudals, the regenerated scales wider than the original scales, which are also distinctly wider than other adjoining scales; scales on limbs often tricarinate; anal scales scarcely, or not, larger than the scales which precede them.

Color in preservative: Above brown or olive brown; a distinct brown band from snout through eye to groin covering three or three and a half scalerows; a whitish line on supralabials involving lower part of ear continued to a point somewhat past arm insertion; no white line on side below brown band: tail generally olive; chin, venter, and underside of tail whitish.

Measurements in mm: Snout to vent, 74; tail, 127; head length, 18; head width, 13; arm, 22; leg, 32; axilla to groin, 35.

A second specimen EHT-HMS No. 31932 agrees with the preceding specimen in having the prefrontals in contact, the interparietal enclosed by the parietals, the supranasals minutely separated, and the frontal touching the second and third supraoculars. There are 31 scalerows around the middle of the body; a lateral brown stripe is present on the side and there is no lateral white stripe bordering it below. The labial markings in the two specimens are nearly identical.

Riopa fernandi (Burton)

- Tiliqua fernandi* Burton, Proc. Zool. Soc. 1836, p. 62 (type locality, Fernando Po); Peters Monatsb., Akad. Wiss. Berlin, 1874, p. 372.
Plestiodon harlani Hallowell, Proc. Acad. Nat. Sci. Philadelphia, vol. 2, 1845, p. 170.
Euprepis striata Hallowell, Proc. Acad. Nat. Sci. Philadelphia, vol. 7, June 1854, p. 98 (type locality, Liberia); Trans. Amer. Philos. Soc., ser. 2, vol. 11, 1857, p. 74, pl. 3, fig. 1.
Euprepis harlani Hallowell, Trans. Amer. Philos. Soc., ser. 3, vol. 11, 1857, p. 75, pl. 3, fig. 2.
Lygosoma fernandi Boulenger, Catalogue of the Lizards in the British Museum, 2nd Ed. vol. 3, 1887, pp. 304-305.

A specimen, EHT-HMS No. 31942, is from Centersite in River Area, Harbel, Liberia, Dec. 20, 1950; Dr. A. E. Weyer collector.

The following characters obtain: rostral presenting a curved convex posterior edge, length of part visible above considerably greater than length of the common suture between the internasals; *paired frontonasal*, both scales broadly in contact with the frontal, in contact laterally with the anterior loreal; prefrontals small, separated from each other by a distance nearly equal to the width of one of them; in contact laterally with both loreals, posteriorly touching the anterior supraocular and anterior supraciliary; frontal widened anteriorly, narrowing posteriorly almost to a point, more than a third longer than its distance from the tip of snout, equal to or greater than the combined length of the parietals; four supraoculars, two bordering the frontal; frontoparietals form a common suture of less than half their length, larger than the interparietal, which with a scale posterior to it, separates the parietals; latter scales much broader than long. Nine supraciliaries, first and last largest; nostril in a divided nasal; no postnasal anterior loreal narrower than posterior and slightly higher; a preocular superimposed above the anterior of two presuboculars; a row of seven or eight suboculars separating labials from the semitransparent scaled lower eyelid; seven supralabials the fifth and sixth below eye; two primary temporals bordered behind by four secondary temporals; a pair of somewhat enlarged scales border parietals behind; ear distinct, oval tympanum deeply sunk, bordered anteriorly within depression by two scales with rounded edges; seven infralabials; mental with a larger labial edge than rostral; undivided postmental touching two labials laterally; first chinshields in contact, second pair separated by a scale; third pair reduced each separated from its fellow by five scales.

Limbs pentadactyle, rather short, when adpressed they fail to meet by a distance equal to width of two scalerows; subdigital

lamellae on fingers simple, short, with a suggestion of a median keel or ridge, 10 under fourth finger; palm covered with smooth rounded, but somewhat raised scales; toes short, the fourth with 16 lamellae bearing irregular longitudinal keels or ridges; sole covered with scales similar to those on palm, the posterior row bordering a row of enlarged scales; no axillary or inguinal depressions or pockets; 33 scalerows about narrowest point of neck, 34 about middle of body; four preanal scales, not or scarcely larger than the scales preceding them; median subcaudals, 87, not wider than adjoining scales; scales from parietal to above vent, 56. All dorsal and lateral scales (except head scales and temporals) with three well-defined keels, the two outer strongest; also rarely, a lateral ridge or tubercle can be seen on scales; scales on lower posterior face of thigh with two tubercles. Venter brownish white, each scale outlined in light brown. On underside of chin and sides of neck some scales are edged with dark brown, forming brown lines on the edges of several rows of scales on the neck. Head nearly uniform dark brown on dorsum, lighter laterally, a black moon-shaped spot below and behind eye.

Color: The ten dorsal scalerows woodbrown, each scale bordered by black leaving the dorsal surface with uniform rows of equal-sized pentagons; the outer scales of the ten may be lighter brown and their outer sides come into contact with a series of black lateral spots or bars; these tend to fuse together on the side of the neck and above the arm to form an elongate, but irregularly edged spot; along the side of the body are eight or nine vertical or somewhat diagonal bars of black, often irregular, sometimes two in contact above or below; scales between bars brownish but lighter than those on the back; lateral caudal scales lighter than those on sides of body with indefinite darker areas dorsally and laterally to the tip; however, towards the latter third the dark scales predominate and there appears a series of bluish-white spots. These whitish spots (in certain lights) can be discerned nearly to the base of the tail but there is small contrast with the other light scales.

Measurements in mm.: Snout to vent, 104; tail, 132; length of head, 21; width of head, 16; snout to arm insertion, 32; axilla to groin, 56; arm, 25; leg, 305.

Remarks: This species may be somewhat aquatic, individuals having been seen to enter shallow water in the rivers. It seems extremely doubtful, as has been proposed, that this is a subspecific form of *Riopa durum* Cope.

Chamaeleon senegalensis Daudin

Chamaeleo senegalensis Daudin, Histoire naturelle générale et particulière des reptiles, vol. 4, 1802-03, pp. 203-209 (type locality, Senegal).

Chamaeleon senegalensis J. E. Gray, Proc. Zool. Soc. London, 1864, p. 471.

A single young specimen is at hand, EHT-HMS No. 31925.

Typhlops leprosus sp. nov.

Type: EHT-HMS No. 31895 Firestone Plantation, Harbel, Liberia, Africa; 1954, collected by Mrs. Dora Weyer.

Diagnosis: A presumed small species having a length of at least 185 mm. the width in length 23-25 times. A preocular present; no subocular; four supralabials; nasal divided, *the suture arising from the lower outer edge of rostral*; gray-white to yellowish, with irregular transverse markings of black and yellowish; 28 scalerows around body at middle, 30 scalerows around body 3 cm. back of snout tip. Scales from mouth to vent 388.

Description of type: Snout prominent, its lower edge with a blunt transverse keel, not hooked; eye clearly visible, the pupil distinct covered by ocular and posterior edge of preocular; rostral large its greatest width 3.4 mm., much less than width of head at level of eyes (5.6 mm.), its posterior edge truncate rather than rounded; prefrontal about 3.5 times wider than long, separating the nasals dorsally; supraoculars minute, touching frontal; latter small, separating the somewhat larger parietals; upper part of nasal reaching to level of middle of eye, widened ventrally the nasal suture arising from lower part of rostral, dividing the scale into two parts; preocular touching second and third supralabials, separated from the supraoculars; part of rostral visible below, much wider than long; ocular touching two labials, the area surrounding eye uniformly light; four scales border it behind, between the fourth labial and the parietal; mental not twice as broad as deep; two infralabials; 30 scalcrows around neck; 28 around middle of body; 20 in front of vent; ventral scales from mouth to vent 388; subcaudals, 8 + 1.

Color: Above gray-white to yellowish with top of head and anterior part of neck dark; neck and body blotched with irregular black spots separated by irregular light yellow areas. All the black scales have a grayish center and these form dim lines of gray through the black but are interrupted by the yellowish blotches between the black areas. Those on the median rows are as distinct as those on the lateral regions. The 15 to 17 ventral rows largely yellowish, with smaller and fewer black blotches, and the light areas in each scale larger.

"Color in life: Surface translucent so that the body is grayish flesh. All pigmented areas are black. The spots on the scales, that give a striated appearance, are gray."

Measurements in mm: Total length, 185; tail, 3.7; width, 3 cm. from tip of snout, 7.6 width at middle 7.8; width into length, 237—25.6 times.

Remarks: The relationship of this form does not seem to be with the other known local species. It differs in the peculiar coloration and in having the nasal completely divided and the nasal suture arising from the rostral. This latter character is known in *anchietae* a form described from S. W. Africa. This, however, has 30-32 scales round the body, and is pale yellow with grayish brown blotches. The nasal is semidivided and the preocular touches only one labial. The length is 119 mm.

Another species that may be related is *Typhlops anomalus* also described from Southwest Africa. This has 28 to 30 scales around the body; however, this species is uniform brown above, the sides and lower parts yellow. The nasal suture arises from the rostral but the scale is only partially divided.

Typhlops manni Loveridge, *Typhlops leucostictus* Boulenger, and *Typhlops punctatus punctatus* (Leach) also are known to occur in Liberia.

It is possible that this form has been described and is to be found among the synonyms of *punctatus*. We believe, however, that the origin of the nasal suture is sufficiently significant to have been recorded, if it were present in any of the forms described. The number of ventral scales is 34 more in *punctatus* from Harbel.

Typhlops punctatus punctatus (Leach)

Acontias punctatus Leach, in Bowditch, Mission, Ashantee, 1819, p. 493 (type locality, Fantee).

Typhlops punctatus Boulenger, Catalogue of the Snakes in the British Museum, vol. 1, 1893, pp. 42-43 (*part.*) ("total length 630 mm."); Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 49, 1923, pp. 45-46; Barbour and Loveridge, in The African Republic of Liberia and the Belgian Congo, edited by Richard P. Strong; Cont. Dept. Trop. Med. Inst. Trop. Biol. Med., no. 5, vol. 2, 1930, pp. 770-772.

Typhlops punctatus punctatus Loveridge; Proc. New England Zool. Club, vol. 17, May 20, 1938, p. 55 (Ganta, R. L.).

Onychocephalus Liberiensis Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1848, p. 59 (type locality, Liberia).

A single specimen, EHT-HMS No. 31890 ♀ has the following characteristics: head much narrower than body, the snout with a very obtuse horizontal keel; nostrils inferior not visible from above; rostral large, the part visible from below much wider than long,

the part visible above two thirds of the width of the head at eye, its posterior edge reaching the front level of eye; latter can be distinguished; nasal narrowed above, much widened below, semi-divided, the suture arising from the first labial, scarcely reaching beyond nostril; the preocular present much narrower than the nasal, somewhat narrower or nearly equal to the ocular, in contact with the second and third supralabial; supraoculars elongate, diagonal, not covering any part of eye, separated from each other; prefrontal three times as wide as long; parietals barely differentiated in size from surrounding scales; frontal smaller than the scale following it; four supralabials; mental twice as wide as long, with two infralabials on each side, concealed when mouth is closed.

The diameter of body at middle is contained in length 22 times; diameter of neck (three centimeters behind head), in length, about 34 times; tail broader than long, the upper part rather sharply deflected downward, the under part slightly turned upward, and ending in a sharp low spine. There are 28 scalerows around body; 30 around neck a centimeter behind tip of snout; scales from mouth to vent, (ventral count) 422; subcaudals, 11 + 1; vent bordered by six scarcely differentiated preanal scales.

Measurements in mm.: Total length, 543; tail length, 10; width of body near middle, 25; three cm. behind tip of snout, 16; width of tail at vent, 15; width of head at back of ocular, 11.

Color: Above generally blackish brown, each scale largely transparent, and showing a dim whitish transverse mark near its middle. These light areas become larger on the sides, some being contiguous and tending to form light lines. The dark brown color forms rows of dots on upper part of sides but lower they become fewer, and the four to six ventral scalerows are uniformly yellowish save for an occasional brown dot. The general impression is a brown snake with ten or twelve lighter lines very dim medianly, but becoming well defined laterally.

Remarks: The stomach contents consisted of recently ingested ant eggs with occasional ants. The mouth contained two ant heads with the mandibles fastened to the mouth tissues.

This species reaches a length of about 800 mm., and is probably the largest species of the genus *Typhlops*.

Loveridge (1938) reports a specimen measuring 795 mm. long, 4 inches in circumference and one and one-fourth inches in diameter, from Ganta, Liberia.

Calabaria reinhardtii Schlegel

Eryx reinhardtii Schlegel, Bijdr. tot Dierk., vol. 1, 1848, p. 2, pl. (type locality, Gold Coast).

Calabaria fusca Gray, Proc. Zool. Soc. London, 1858, p. 154, pl. 14 (type locality, Old Calabar, Southern Nigeria, W. Africa).

Calabaria reinhardtii Boulenger, Catalogue of the snakes in the British Museum, vol. 1, 1893, p. 92, ("Liberia to the Congo"); Proc. Zool. Soc. London, 1919, pts. 3-4, Feb. 1920, p. 274; Stull, Proc. Boston Soc. Nat. His., vol. 40, no. 8, p. 396; Barbour and Loveridge, Cont. Dept. Trop. Med. Inst. Trop. Biol. Med., no. 5, 1930, p. 772 (Paiata, St. Paul's River, Liberia).

Two specimens of this burrowing boid serpent, EHT-HMS Nos. 31887 ♂—31888 ♀ from Harbel, Liberia, are at hand. The characters of No. 31887 follow: the rostral is about as wide as high the part visible above about as long as wide; this scale followed by three paired scales wider than long, the first two in contact mesially, the third separated by a small scale; two supraoculars, frontal and parietals considerably broken; nostril in a single nasal, not or only partially divided, followed by a rather large loreal (a small scale segmented from the third median pair forms a second superimposed "loreal" on one side); one preocular, two postoculars (one only on right side); two or three anterior temporals; supralabials, 7-8, the third and fourth bordering orbit; infralabials, 9-10, the first three touch the small anterior chinshields, the first pair in contact mesially; second chinshields not distinguishable from the chin scales, of which there are seven rows between the chinshields and the first ventral. Scales smooth, with formula, 31 head, 25 neck, 29 middle, 23 (24) anterior to vent; ventrals 221, anal single, subcaudals 1 pair, + 19 single + 1 single terminal. The tail is blunt.

Color: Above lavender brown with many scattered lighter scales or groups of scales; entire head and first part of neck blackish; upper part of latter half of tail black; venter largely cream-white with some small black marks.

Measurements in mm., of Nos. 31887 and 31888 respectively: total length, 822, 728; tail, 62, 56; head width, 17, 14; width of neck, 19, 15; greatest width of body, 30, 24; width of tail (at 15 mm. from tip), 21, 16.

Remarks: "Very common here, usually seen crossing road of the house areas at night or in the early morning especially at the beginning of the dry season. One was found dead on the cement air-strip curled in a typical manner and only recently dead. Since it appeared uninjured we surmised it was unable to burrow into the cement and the hot sun had killed it.

"We kept one alive for a while. It was very gentle and my young daughter often carried it about. It always curled in a ball with the head carefully tucked in the center, but the tail was left poking out as though it was the head, and could fool anybody. When it was put down it remained motionless for ten minutes or so, then would cautiously uncurl and very slowly move away to escape. Obviously it was incapable of fast movement. The muscles are so strong that it was very difficult to unroll it by force. It never hissed, threatened, or thrashed about.

"There are two color phases in life represented by the two specimens. (1) Dorsal color dark brown with individual scales or small groups of scales medium brown or tan; ventral surface with cream mottling, spotted with medium brown. (2) dark brownish purple, the markings orange or orange shaded purple. Particularly toward the posterior part, the orange is very bright and striking both dorsally and ventrally.

"The amount of light color on the tail varies a great deal in the species, many specimens I have seen showing none, others much."

If the preserved specimens are removed from alcohol into the air for as short a period as five minutes, the entire ventral surface changes to a uniform paper-white color and certain of the scales adjoining them also assume this color!

The limb remnant is terminated by a sharp protruding claw.

Variation: The smaller specimen has 226 ventrals, an undivided anal, and the subcaudals as follows: one divided pair followed by 24 unpaired scales.

There is a small intercalated scale between the second and third infralabials bordering lip, that is absent in the smaller specimen. The posterior infralabials in both appear to be segmented from the adjoining scales. The smaller female specimen has two postoculars on each side, and has no trace of the limb externally.

Neusterophis variegatus (Peters)

Mizodon variegatus Monatsb. Akad. Wiss. Berlin, 1861, p. 358. (type locality, Pel, Gold Coast, Africa)

Neusterophis variegatus Loveridge, Proc. U. S. Nat. Mus. vol. 91, no. 3128, 1941, p. 120. (Gibi, Bromley, Bendaja, in Liberia)

A single specimen, EHT-HMS No. 31918 has the following characters all included in the known variation: length of eye equal to distance between eye and tip of snout; scalerows, 15, 15, 15; ventrals, 130, subcaudals (divided), 76; anal divided; scales smooth, lacking apical pits; temporals 1 + 2; preoculars, 2-1; postoculars,

3, supralabials, 8, the fourth and fifth bordering orbit; nasal divided; loreal higher than wide; infralabials, 8-9, the last small, four touching the anterior chinshields, which are much shorter than the second pair. There are 24 maxillary teeth (counting missing teeth).

On middle scalerows dark brown, each scale with indefinite lighter flecks; on each side a row of whitish dots, none as large as a single scale, each separated longitudinally from nearest dot by about two scale-lengths; lower scalerows marked like those on dorsum; median half of venter yellow with the outer fourth of each ventral bearing a regular quadrangular dark spot, usually a little darker than body color; median subcaudal area similar to median ventral area; labials yellowish, the sutures edged with black.

Natrix anoscopus anoscopus Cope

Tropidonotus anoscopus Cope, Proc. Acad. Nat. Sci. Philadelphia 1861, p. 299; (type locality, Cuba, *ex errore*).

Natrix anoscopus Cope, Proc. U. S. Nat. Mus., vol. 14, 1892, p. 673.

Natrix anoscopus anoscopus Loveridge, Proc. U. S. Nat. Mus., 1941, pp. 118-119 (Gibi, Bendaja, Harbel, Paiata, R. L.).

Tropidonotus ferox Günther, Ann. Mag. Nat. Hist., ser. 3, vol. 12, p. 355, pl. 6, fig. F (Fernando Po.).

Helicops gendrii Boulenger, Ann. Mag. Nat. Hist., ser. 3, vol. —, 1910, p. 512 (French Guinea).

Natrix anoscopus gendrii Loveridge, Proc. U. S. Nat. Mus., 1941, pp. 118-119.

Loveridge has recognized two subspecies, *anoscopus anoscopus* and *anoscopus gendrii* but suggests that the form on Fernando Po described as *ferox* could not be given subspecific rank. In the collection at hand there is a *Natrix* that agrees in very considerable detail with Günther's figure of *ferox* but differs from that form in having the lateral markings absent, the color being a dull grayish-brown, without lateral black spots. There are no lines of spots on the venter which is orange-tan, each scale edged anteriorly with a blackish line.

It would appear probable that this is a subspecific form of *ferox* [= *anoscopus*] but it must be very doubtful that it represents the typical form *anoscopus anoscopus*, a species having, presumably, an erroneous type locality "Cuba."

The specimen at hand is EHT-HMS No. 31893 ♀, from Harbel, Liberia. It has the following characteristics: the part of rostral visible above more than a narrow transverse line; a pair of small internasals only minutely longer than wide; prefrontals wider than long, a little shorter than internasals; frontal short, scarcely longer than wide, slightly less than its distance to tip of snout, distinctly

shorter than parietals; nostril in a single nasal, an entrant suture from first labial partially divides the scale but does not reach nostril; loreal longer than high; two preoculars, two postoculars, three or four suboculars; supraoculars slender; temporals, $1 + 2 + 4$; supralabials, 9-9, none entering orbit; infralabials, 10-10, five bordering first pair of chinshields, which are smaller, but equally as long as the posterior pair. Scale formula, head 35, 23, 25, 25, 20; all scales strongly keeled with apical pits; ventrals, 141; anal, divided; subcaudals, 68. The ventral preceding the anal pair is divided; a small intercalated scale also present between this and the anal pair.

Color: "In life entire dorsal surface dull grayish-brown; no black lateral markings; there are a few small lateroventral black flecks low on the side near ventrals; ventral color orange-tan each scale bordered anteriorly with a dark transverse line; subcaudals gray."

The top of the head is uniform olive to gray brown, the edges of the upper labials being somewhat darker; infralabials and the scales and shields on chin and throat edged with gray; occasionally there may be a tiny black border on outer edge of ventrals.

Measurements in mm: Total length, 524; tail, 131; width of head, 14; length of head, 20; narrowest neck width, 11.4; length of frontal, 4.5; width of frontal, 3.5.

Remarks: This group of *Natrix* has a deep groove between the labials and temporals, which is more or less continued between labials and the suboculars and loreal. In the groove one finds a narrow expanse of gray skin when the labials are pulled down; when seen from above the posterior upper part of labials form a tiny shelf.

"The specimen was caught while we were tearing down a fish pond. It was taken with a two and one-half inch *Tilapa* (a pond fish) in its mouth."

Natrix firestonei sp. nov.

Type: EHT-HMS No. 31894 Harbel, R. Liberia, Mrs. Dora Weyer collector, 1956.

Description of type: Rostral twice as broad as high, visible above as a line; internasals narrowed anteriorly, much longer than wide; prefrontals shorter and wider than the internasals; nostril in a single nasal, with a small suture entering the scale from the first labial but not reaching nostril; loreal longer than high; frontal longer than wide, longer than its distance from tip of snout, shorter than the parietals, one preocular not reaching the frontal; three or four suboculars separating all labials from orbit; two postoculars; temporals,

1 + 2 + 3, the anterior elongate, others scalelike; supralabials, 9, separated from temporals by a noticable groove; infralabials, 10-9, five scales touching the elongate anterior chinshields which are slightly longer than the second chinshields; latter scales separated by small scales; two pairs of scales between chinshields and first ventral.

Scales sharply keeled, those on outer row are smooth; the scale formula, 28 (head), 23, 23, 20, (the median row lost one centimeter anterior to vent). Apical pits paired; ventrals, 143, the last one separated from the paired anal by two scales not in contact mesially; subcaudals, 67.

Color in life: Dark brownish-gray dorsally; five rows of black spots, the median series alternating (usually) with paired lateral spots that are a little higher than wide; below these on the border of the ventrals another, more numerous series of smaller spots varying in size. Head generally dark grayish to blackish; grayish below with parallel lines of dark brown spots tending to form two more or less continuous lines near the outer part of ventrals on the anterior two thirds of body, the area between them gray; the edges of the ventrals with some brown along their anterior edges; spotting on tail much less distinct; dark gray in subcaudal region. Scales on chin and throat more or less outlined in brown or black.

Head relatively slender not strongly differentiated from neck.

Measurements in mm: Total length, 472; tail, 113; width of head, 10; width of neck, 8.2; head length 18.4; length of frontal 4.25; width of frontal 3.0.

Remarks: Body triangular in cross-section with a rather distinct median dorsal ridge. The specimen is a female with seven eggs showing no trace of embryos. This specimen was captured some distance away from the water. The paired apical pits are relatively large and distinct over most of body and tail. There are 23 maxillary teeth, the posterior ones only a little stronger and larger than the anterior, with no diastema present.

Since this and the preceding snake occur in the same locality, it does not seem fitting to regard one a subspecies of the other. The scale formula is similar, the chief differences being in the different shape of the head, which is much wider in *anoscopus*. There is a distinct difference in the color pattern; and the somewhat elevated median line and somewhat triangular body is seemingly very different from the rounded body of *aniscopeus*; the proportionally larger temporals and parietals are significant also.

"This specimen was not found in or near water. The snake is thinner, the head longer and narrower and the snout more rounded than in our specimen of *N. aniscopus aniscopus*."

Bothrophthalmus lineatus lineatus Peters

Bothrophthalmus lineatus Schlegel, in Lichtenstein and von Martens, Nomenclator Reptilium et Amphibiorum Musei Zoologici Berolinensis, 1856, p. 27 (*nomen nudum*; type locality, Goldküste); Barbour and Loveridge, The African Republic of Liberia and the Belgian Congo. Cont. Dept. Trop. Med. and the Inst. Trop. Biol. and Med. no. 5, 1930, p. 784. (Cambridge, Harvard Univ. Press).

Elaphis (Bothrophthalmus) lineatus Peters, Monatsb. Akad. Wiss. Berlin, 1863, p. 287 (type locality, "Guinea").

Bothrophthalmus lineatus lineatus Loveridge, Proc. New England Zool. Club, vol. 17, May 20, 1938, p. 56 (Ganta, Republic Liberia).

This brilliantly marked serpent is represented by a single specimen EHT-HMS No. 31891 ♀. It has the following scale and other characters: rostral very narrowly visible above; internasals small, somewhat elliptic or leaf-shaped; about one third of size of prefrontals; frontal longer than wide, equal to its distance from tip of snout, as long as the parietals; inner part of the supraocular fused to the parietals; nasal divided; a longitudinal trenchlike depression, having a sharp canthal edge above in loreal region is continued behind lower posterior part of eye for a short distance; loreal large elongate, somewhat rectangular on left side, vertically divided on right side; a preocular, the upper part of which grows forward above posterior half of loreal;* two postoculars; two anterior temporals, only one, however, in contact with postoculars; two secondary temporals; seven supralabials the fourth and fifth border orbit, the upper edge of the fourth bent so as to resemble a lower preocular; seven infralabials, four touching first pair of chinshields, which are larger than the second pair; scale formula, 27 (head); 23, 21, 20. Ventrals, 194; subcaudals, 71; anal single; all scales keeled, the posterior dorsal keels forming continuous ridges.

Color: Body striped in black and red. There are four black stripes, the two median wider than the intervening red stripes, the outer stripes of about width equal to the adjoining red stripes; on the third scalerow there is a series of dashlike marks forming a more or less continuous line; the head has five lines, two through eye, a pair of lines passing above the eyes and a short frontal-occipital line. All stop and are separated from the body lines by a short diastema; a few dim dark spots on infralabials and on neck; some pigment present on the posterior subcaudals.

* This must be examined carefully since the anterior part resembles a second loreal and may be mistaken for a separate scale.

"A beautiful animal! I saw it immediately after death—the lateral and dorsal areas between the back stripes were bright "orangish" brick-red, the dorsal head color darker. The ventral surface was a lovely iridescent vermilion-pink, the tip of the tail a darker shade. The head ventrally was white with scattered orange spots."

Remarks: "This snake though harmless is held by many natives to be deadly poisonous and by others a snake that foretells death. All regard it as 'bad-bad' and wanted us to have nothing to do with it. It apparently holds a place in their superstitions much like that of the chamaeleon. Dr. Harley in his book, 'Practice of Native Medicine' describes the special medicines used for the 'red and black snake' by which I think he means *B. lineatus lineatus*."

The specimen is a female containing eight ovarian eggs.

Boaedon lineatus virgatus Hallowell

Coelopeltis virgata Hallowell, Proc. Acad. Nat. Soc. Philadelphia, (vol. VII), 1854, p. 98 (type locality, Liberia).

Boaedon virgatus Boulenger, Catalogue of the Snakes in the British Museum (Natural History), vol. 1, 1893, p. 331. (spelled *Boodon*) (synonymy); Bogert Bull. Amer. Mus. Nat. Hist., vol. 77, 1940, p. 24, (Ganta, Liberia).

Three specimens EHT-HMS Nos. 31913-31915, all females, yield the following data respectively: ventrals, 213, 211, 218; subcaudals 47, 47, 45; anal single; scalerows, 21, 23, 17; 21, 23, 17; 21, 21, 17; preoculars, 2-2, 2-2, 1-1; postoculars 2-2; preocular touches frontal, no, yes, yes; supralabials, 8-8 in all; supralabials border orbit, 4th, 5th, in all; infralabials, 9-9, 8-8, 8-8; total length in mm., 806, 350, 408; tail, 104, 43, 45. In all there are two lines on the side of the head, and a light mark on the rostral extending down across chin. The venter is lavender-gray with a line of cream in the middle. The pitting on the scales is paired throughout save an occasional scale on the outer row with a single "apical pit." No. 31913 contains six eggs.

"The color of the entire dorsal surface is glossy black. There are two sets of yellow lines on the side of head; the lateral surface of the head between the yellow lines is dark gray. Ventrally, the head is grayish white with a pinkish wash. This narrows at the neck into a cream-yellow stripe running the length of the body and widening to include the entire anal scale, and making a prominent cream-yellow spot.

"The remainder of the ventral surface and the subcaudal area is dark glossy gray. A second adult specimen which I have here for

the hospital collection has the ventral stripe peach-yellow and the immature which I send had, in life, a pink-orange ventral stripe heavily shaded with black in the posterior half of the body. All were *black* dorsally, not *brown with a gray head* as it is sometimes described."

Boaedon lineatus lineatus Duméril, Bibron, and Duméril

Boaedon lineatus Duméril, Bibron, and Duméril, *Erpétologie générale*, vol. 7, pp. 363-364 (type locality, Gold Coast).

We cannot regard this species as subspecifically related to *Boaedon virgatus* Hallowell. The two occur together and are separable on the basis of several characters. For example, markings, ventral coloration, number of dorsal scalerows, and the character of the apical pits. One specimen, EHT-HMS No. 31916 ♀ in the collection contains a rodent, *Rattus rattus* * with a total length of 352 mm.

The following characters obtain: rostral narrowly visible above; internasals subtriangular, about as wide as long, fused together anteriorly for a short distance; prefrontals about as long as wide; frontal subtriangular about four-fifths times as long as wide, touching the preocular, slightly longer than its distance to snout tip, shorter than the parietals but equal to its distance from their posterior tip; nasal completely divided, the anterior part much wider than posterior, rather narrowly separated from its fellow from the opposite side; loreal more than twice as long as high; one large preocular touching two infralabials; two postoculars, only the lower touching anterior temporal; temporals, 1 + 2 + 3; supralabials, 8-8, the fourth and fifth bordering orbit; infralabials, 9-9, four touching the first chinshields, which are larger than second pair; no scales between either pair of chinshields; eye rather small, pupil vertical; scalerows, 33 about head, 27 neck, 29 middle of body, 21 anterior to vent; scales of the median rows with single apical pits; scales of the five outer rows with double terminal pits, except outermost, which also have a single pit. Ventrals, 220; subcaudals, 49 (divided); anal single. Maxillary teeth 18, the fourth and fifth largest, diminishing posteriorly; no diastema.

Measurements in mm.: Total length, 851; tail length, 102; length of head, 29; width of head, 21.

Color markings: Above lavender to violet with a cream line from

* Identified by Mr. Philip W. Ogilvie.

rostral through the upper part of eye to lower tertiary temporal; a second line, beginning on first supralabial, to eye, and from eye to last supralabial; the anterior part of the line dim; an arched light line on rostral, the two ends directed downward across mental and first infralabial; a light line begins opposits the fourth ventral and extends to level of the 57th ventral; chin and throat grayish; venter and subcaudal region white, save for a faint pigmentation on extreme outer edges of the ventrals.

Bogert (1940) has recognized several subspecific forms in this species. He regards the typical form, (type locality Gold Coast) with two lateral white lines as occurring in Tanganyika, Nyasaland, Belgian Congo, Natal, and Angola. This large series might profitably be examined for apical scale-pit characters. Since Bogert does not comment on the color and markings of this series one presumes that they tend to agree with the type.

My specimen does not agree with the type in color markings so far as concerns the two lateral body stripes.

Chlorophis heterodermis (Hallowell)

Chlorophis heterodermis Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1857, p. 54 (type locality, Gaboon).

Three specimens of this snake are at hand: EHT-HMS Nos. 31920, 31921, 31922, all females. The following characters obtain in the three specimens respectively: Total length, in mm. 670, 541, 527; tail, 172, 142, 138; ventrals, 152, 149, 149; subcaudals, 81, 79, 79; anal single in all; supralabials, 9-9, the 4th, 5th, 6th, entering orbit in all; infralabials, 9-9, 9-9, 10-0, the first five touching the first pair of chinshields.

The scale formula is 15, 15, 11 in all. The scales are smooth but in No. 31920 pits are present on the anterior part of the neck. Some scales have 3 apical pits, others two, others one only or none. The apical pits on No. 31921 are more pronounced and extend back on neck for several inches.

In 31922 the epidermis of the scales is lost and apical pits are dim or absent. No. 31920 is uniformly black above in preservative, the side of the snout and a postorbital labial spot, white; chin and anterior part of throat yellowish to ivory-white, the yellow and black interdigitating to some extent on the sides of the neck. The ventrals are keeled laterally but the subcaudals lack keels. The maxillary teeth are 35-34 in No. 31920.

Mehelya poensis (A. Smith)

Heterolepis poensis A. Smith, Ill. Zool. South African Rept., 1847, footnote to pl. LV (type locality, Fernando Po).

The single specimen EHT-HMS No. 31884 ♂ has the following characters: rostral visible above as a narrow band; internasals wider than long; prefrontals twice area of the internasals, longer than wide, touching loreal laterally; frontal small, subtriangular, the front edge curving somewhat, distinctly shorter than its distance to the end of the snout, much shorter than the parietals, double the width of the supraoculars; parietals angulate posteriorly; nostril between two nasals; loreal longer than high; one preocular, two postoculars; temporals, 1 + 2 + 3; supralabials, 8-8, the third and fourth bordering orbit; infralabials, 8-8, the first five touching the first chinshields, which are distinctly larger than second pair; median scalerow enlarged, bicarinate, the scales somewhat hexagonal; other scales with single keels; scale formula, 19 (head), 15, 15, 15; ventrals, 240; tail broken, partly missing; anal single.

Color in preservative: Uniform lavender brown above on sides and on outer edges of ventrals. Venter and subcaudal region uniform white; edges of supralabials and infralabials white.

Approximate total length, 857 (tail broken); snout to vent, 691.

Boiga blandingii (Hallowell)

Dipsas blandingii Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1844, p. 170; *idem, ibid*, 1854, p. 100 (type locality Liberia).

Dipsadomorphus blandingii Boulenger, Catalogue of the Snakes in the British Museum (Natural History) vol. III, 1896, pp. 77-78 (synonymy).

Boiga blandingi Cope, Proc. Acad. Nat. Sci. Philadelphia 1860, 264; Barbour and Loveridge, in Contributions from the Department of Tropical Medicine and the Institute for Tropical Biology and Medicine No. V. Harvard College Press, Cambridge, 1930, p. 773 (Paiata, St. Paul's River); Loveridge, Proc. U. S. Nat. Mus.; vol. 91, p. 122. (Bromley); Proc. New England Zool. Club, vol. 17, May 20, 1938, p. 59 (Ganta, R. L.).

A large specimen EHT-HMS No. 31886 ♀ Harbel, Liberia, has the following scale characters: rostral scarcely visible above, wider than high; internasals little more than half the area of the prefrontals; frontal short, as wide as long, equalling its distance from snout tip, somewhat shorter than the parietals; eye large, prominent; nasal divided, the posterior part the larger with a depression; a loreal; two preoculars, the upper not touching the frontal; two postoculars; two anterior and two secondary temporals; supralabials nine, the fourth, fifth, and sixth bordering orbit; the seventh and eighth touching the lower postocular; infralabials, 13-13, four or five touching first chinshields, which are nearly same size as second

pair; a pair of scales between second chinshields and first ventral. Scale formula, 34 (head), 29 (neck), 23, 23, 17, 15, the median row enlarged, more than double the size of scales in adjoining row; ventrals, 266; anal divided; subcaudals, 125.

The tooth formula is $9 + 2 + 1$; $10 + 2 + 1$. The anterior teeth increase from first to fourth then are nearly equal; the two fangs stand one behind the other, their grooves deep and open the length of the tooth; a third fang, after a short diastema shows traces of a groove but is not open except at tip and base. The dental formula taken from a head of another specimen EHT-HMS No. 31945, is, $10 + 2 + 1$, $10 + 2 + 1$. In this specimen there is a suggestion of a groove but no apparent opening capable of conducting venom can be discerned on the last fang.

Measurements in mm: Total length, 2357 +; tail, 525 +; snout to vent, 183.

Color in life: "Dorsal ground color grayish tan, the diamond-shaped markings darker tan, outlined in brown. A dark brown collar one scale wide around neck. Dorsal head color a darker grayer tan than body, the mottlings dark brown; supralabials edged with some dark brown. Ventral surface of head and neck pale grayish green; five inches behind head this merges into gray with a greenish cast; at 16 inches behind head it becomes plain tan, continuing so to the tip of the tail."

Remarks: "This snake was found electrocuted at the hydroelectric plant with a large black snake. It would appear that the latter had been chasing it when they came into contact with the electric wires. The natives all insisted that the black snake eats this species."

The stomach contains three young birds, one subadult and two nestlings of *Spermestes cucullatus cucullatus*.*

Psammophis sibilans phillipsii (Hallowell)

Coluber Phillipsii Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1844, p. 169 (type locality, Liberia).

Psammophis sibilans phillipsii Loveridge, Bull. Mus. Comp. Zool. Harvard College, vol. 87, no. 1, Oct. 1940, pp. 41-44. (monographic review; bibliography)

This species is represented by two complete adult specimens EHT-HMS 31940 ♀ 31941 ♂ and two heads 31908-31917; also by four hatchlings Nos. 31909-31912 two associated with the egg. We have followed Loveridge (*loc. cit.*) in regarding *phillipsii* a subspecies of *sibilans*. The specimens so far as can be determined

* Identified by Phillip Ogilvie.

agree with the limits of variation given by Loveridge, all of the complete specimens having a single anal plate.

There is a considerable difference in color patterns in the four hatchlings. Three have the labials and many chin scales bearing black spots. In No. 31912 the lips and chin lack all black spots, the venter is darker, and the tail is lighter than in the other three specimens. This one has a combined ventral-subcaudal count that totals 283. This is considerably higher than the counts in the young with complete tails, which are 264, 269.

"This snake is, next to *Causas rhombeatus*, the commonest snake here by all means. It is seldom seen in the rainy season, but as soon as the dry season gets under way in late December or January they are found around every house or open grassy spot.

"They have most interesting breeding habits; all stories told me by planters agreeing with the one nest I saw myself. In this last case, Dr. Kessler phoned me to come to his house saying that the boys had found a 'nest of snakes.' I went immediately and found the boys of the yard crew waiting for me. They had, in hand, obviously just killed, eight large snakes of this species, and they (and he) claimed that they had found them all entwined together in this hollowed out spot in the lawn. The spot was about a foot and a half in diameter when I saw it, about one foot deep, and so badly cut by the boys' cutlasses I couldn't tell what it must have looked like before they found it. However, they had 'squashed' beside it a mess of snake eggs, how many I couldn't tell exactly. I counted, uncrushed and still in the hole where Dr. Kessler had had them leave the rest for me to see, 52 eggs. This was obviously a communal nest. Because of the mess—you can imagine eight yard boys killing eight big snakes with cutlasses—I did not examine the snakes for sex, as I later wished I had. How many eggs might eventually have been laid I don't know either. However, I have had several planters tell me of finding similar nests on their own lawns—always the estimate of the numbers of snakes present together is between eight and ten. The largest head of this species, in the specimens I sent you, incidentally, came from this 'nest.'

"As to the color, the 'greenness' of the back varies considerably in individuals, so that sometimes one calls it a 'brown snake' and sometimes a 'green snake,' varying, in other words, from a dull olive-brown to a bright olive-green, and sometimes a distinct gray-green with no tint of olive. Ventrally the green is always striking, sometimes a clear, light-green, sometimes bluish green,

sometimes, yellow-green. There is also considerable variation in the amount of orange. In all specimens there is some orange along the side of the head and on the inferior labials. In one of the specimens I sent you, you will see orange over the entire nose and mouth area with only the chinshields and the gulars white, the orange extending over the rostral, nasals, loreals and preoculars. In some specimens this orange area of the jaws is spotted with black, in others not. In some the orange continues down the first ventral plates also, and in the one you have, it runs the length of the body on the outer scalerow and above the upper (outer) edges of the ventrals, the anal area and the ventral side of the tail being quite orange. In all specimens I have seen there is some yellow or orange on the under part of the tail, in some the orange being very bright everywhere but on the vertebral row dorsally. There is also considerable variation as you see in your specimens on the black markings dorsally."

Thelotornis kirtlandii kirtlandii (Hallowell)

Leptophis kirtlandii Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1844, p. 62, *idem, ibid.*, 1854, p. 100. (type locality, Liberia).

Thelotornis kirtlandii Barbour and Loveridge, Cont. Dept. Trop. Med. No. V, vol. II, 1930, p. 773. (Gbanga, Liberia).

Thelotornis kirtlandii kirtlandii Loveridge, Bull. Mus. Comp. Zool. Harvard College, vol. 95, no. 2, Dec. 1944, pp. 149-154 (Edina and Gbanga, Liberia) (literature listing).

A single specimen (EHT-HMS 31885 ♀) has the following characters (due to an old head injury certain characters cannot be determined): head wedge-shaped; rostral much broader than high; eye large; internasals as long as wide, touching one loreal; prefrontals longer than internasals, bordering two loreals laterally; nostril in a single elongate nasal; two loreals, the second twice the length of first; one large preocular, not touching frontal; three postoculars, the lower elongate; temporals, 1 + 2; a pair of postparietals separated by a scale; supralabials, 8, the fourth and fifth bordering orbit; infralabial, 9-10, the first four touch the first pair of chinshields, which are shorter than the second pair; scale formula, 19-19, 15, the scales weakly keeled, elongate. Ventrals 178; anal divided; subcaudals 141.

Color: The head is uniform lavender (probably green in life) the labial areas somewhat lighter; neck indefinitely barred with grayish blotches growing less distinct posteriorly; most of body light lavender with dark flecks indistinctly outlining spots.

Aparallactus modestus Günther

Elapops modestus Günther, Ann. Mag. Nat. Hist., ser. 3, vol. 4, 1859, p. 111, pl. 4, fig. c (type locality "West Africa"); Zool. Record, 1864, p. 152. (figured by Jan as *Elapops petersii*); Boulenger, Proc. Zool. Soc. London, Feb. 20, 1920, pl. 293.

Pariapsis plumbeatra, Cope, Proc. Acad. Nat. Sci. Philadelphia, 1860, pp. 241-242 (type locality, Liberia).

Elapops plumbeater Cope, Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 566 (contrasts *plumbeater* with *modestus*).

Our specimen, EHT-HMS No. 31892 ♀ from Harbel, Liberia, has the following characteristics:

Rostral well visible on dorsal part of snout, one and one-third times wider than high; internasals small, less than half the area of the prefrontals; frontal wider anteriorly, longer than wide, its length greater than its distance from tip of snout, distinctly shorter than the parietals; latter slender, pointed behind, fused together at tip; nasal divided, the nostril chiefly in the very small anterior part; no loreal; one preocular; two small postoculars; eye diameter less than its distance from the lip; no anterior, but two posterior temporals, the upper very large; supralabials seven, the third and fourth border orbit; fifth much the largest, broadly in contact with the parietal; infralabials six, three bordering the first chinshields, which are wider and equally as long as the second pair; upper temporals separated behind the parietals by three scales; two paired scales between second chinshields and the first ventral.

Scales smooth, without pits, in 15 scalerows throughout neck and body, the outer row a little larger than the others; ventrals, 158; anal divided; subcaudals, 35 in a single row. (Tip of tail missing.)

Color in fixative: Dorsally and laterally bluish gray, each scale with a more or less distinct dark border; head generally slightly more ultramarine; supralabials a little lighter near edge of lip; ventral surface dirty whitish, each scale with a line of grayish pigment on its anterior edge, growing more pronounced posteriorly where it may spread over the entire scale; subcaudals uniformly grayish black.

Measurements in mm: Total length, 454; tail (incomplete), 58; width of head, 9; width of body, 10; head length, 13.

Remarks: Although reported by Cope (1860) from Liberia under the name *Pariapsis plumbeatra* (*sic*) it was not included in the Barbour and Loveridge list (1930). It would appear that it is a relatively rare snake, the greater part of its range being east and south of Liberia.

The curiously pointed condition of the parietals is seemingly caused by their fusion posteriorly with the scale normally partially separating their posterior tips. The normal suture between the parietals stops at the point of fusion.

Naja melanoleuca Hallowell

Naja haie melanoleuca Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1857, p. 61 (type locality Gaboon, West Africa).

Three specimens, two young, and the head and neck of a half grown individual, are in the collection. These are EHT-HMS Nos. 31905, 31907, and 31906 respectively. The scale characters of the young respectively are as follows: ventrals, 210½, 214; subcaudals, 64, 68; scalerows, 23 (24) neck, 17, 13; 23, 17, 13, the scales smooth without pits; supralabials, 7-7, 7-7, the fifth highest, the third and fourth bordering orbit; infralabials, both 8-8; preocular, both 1-1; postoculars, both 3-3. Total length in mm., 633, 432; tail, 106, 78.

The coloration of the young (No. 31905): above blackish the top of the head a little less dark, the sides light grayish white or yellowish white, the labial sutures more or less bordered with black. At a distance of about 30 millimeters back of parietals and again at about 65 and 120 mm. many of the black scales have small yellowish dots near their anterior borders and the yellow of certain ventral bands of yellow encroaches on the outer scale rows. The chin and neck for about 57 millimeters is yellowish white; this followed by a black bar, 21 mm. long (9 ventrals) then follows a yellowish white band 25 mm. long with a single black ventral in its middle; the following black band is 29 mm.; beyond this the scales are gray black for some distance then become intense black to the end of the tail. No. 31907 shows only two yellow areas on venter separated by a black band 11 mm. wide. The sides of the neck in both show a few small black spots. Tail banded with a minute yellow band very near tip.

"This is a very common snake here, probably third in order in frequency of occurrence. The young are speckled with white when alive. I have seen four live ones in my garden at various times—specimens between one and two and a half feet in length and they all show this speckling noticeably, so that the first time I thought it was a different species until it spread its hood. The adults when alive show no white at all, but when preserved the scales separate a bit and show a little. Incidentally, the young have always, in my

experience, been more vicious than the adults, which usually try to get away although they turn and spread their hood when attacked. But the little ones usually turn and spread the hood when first disturbed and do not take advantage of a chance to escape. Also, they do not appear to be fast-moving snakes as many accounts state. I personally found a large one in my chicken house and had plenty of time to dodge his attacks and when he slipped through the fence, I was able to run around the enclosing fence and catch up and kill him on a downhill run to the rubber trees. He had not eaten and was not sluggish on that account. In motion they remind me of the common pilot black snake I grew up with in Ohio. Incidentally, they love eggs, and are often found around chicken houses, I presume mainly hunting rats, but certainly several here to my knowledge have been killed when they had been found asleep, usually under a setting duck, with three or four eggs inside."

Atractaspis corpulenta corpulenta (Hallowell)

Brachycranion corpulentum Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1854, pp. 99 (type locality, Liberia).

Atractaspis corpulentus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 1857, p. 70 (correction of type locality); Boulenger, Catalogue of the Snakes in the British Museum (Natural History), vol. 3, 1896, p. 514.

Atractaspis corpulenta corpulenta Laurent, Mem. Inst. Roy. Sci. Nat. Belgique, ser. 2, fasc. 38, 1950, pp. 40-42 (synonymy).

Description (EHT-HMS No. 31889 ♂ Harbel, Liberia): Rostral large, part visible above wider than long, the length equal to its distance from frontal, partially separating the internasals; latter a little wider than their greatest length; prefrontals shorter but wider than internasals, their common suture slightly greater than that between internasals; frontal *wider than long*, equal in length to its distance from tip of snout, a little shorter than parietals; supra-oculars very small; nasal divided, the posterior scale more than double the size of the anterior; no loreal; a very small preocular and a small postocular; eye small, separated from the mouth by a distance equal to a little more than three times its diameter; a very large anterior temporal; three secondary temporals all less than half the size of anterior; five supralabials, first small, the third and fourth border orbit; a small mental; first infralabials in contact behind mental, but separated by the first chinshields, which border lip, from the second infralabials; five infralabials; second chinshields small separated by three rows of scales; the second infralabial very large; seven scales between first chinshields and first ventral. Snout wedge-shaped, with a somewhat depressed transverse edge. Scale

formula: 28 (head), 23, 21, 17; ventrals, 190, subcaudals, 26-27, part double, part single as follows, 1 paired + 7 single + 2 paired + 1 single + 4 double + 2 single + 9 paired + 1 terminal (single), (the last paired scales separated). The terminal subcaudal is a short conical spine; anal single; scale smooth without apical pits. A row of median widened scales occupying the dorsal tail surface, about 12 in all.

A pair of functional fangs on maxillary; other teeth greatly reduced.

Color: Blackish brown above, slightly lighter on sides and venter; posterior part of tail white, the color extending more than half its length on ventral part, less than half on the dorsum.

Measurements in mm.: Total length, 619; tail, 58; width of head, 20; width of body, 21; head length to back edge of parietal, 16.

Remarks: "I have so far found or been given a total of three *Atractaspis corpulenta*, whereas, so far at least, none of the other *Atractaspis* species have been seen. My collectors tell me that another kind, similar to these but different, can be found up-country near Salala. That region has a much drier climate and more sandy soil.

"I came across a live specimen lying injured in a ditch beside the road early in the morning (apparently it had been hit a glancing blow by a passing car) . . . and observed how it behaved. It flattened its body making itself appear to be a much heavier snake than it was, and added to this effect by inflating the neck region considerably. Then the small head was curved down while the neck was reared up, giving it a very vicious appearance for so small a snake.

"All of the specimens are dull black or grey-black. Leeson's book states that they are a slaty blue."

The type description of *Brachyranion corpulentum* by Hallowell shows several differences from the generally accepted idea of this species. For example, the following are recorded for the type: scale rows about body 25; internasals and prefrontals united into one pair of scales; subcaudals single; there are but four supralabials. Laurent (1950) in his revision has not commented on this discrepancy. I am not aware of this condition occurring in any other specimen (Boulenger 1906 only suggested it might be an anomaly). It seems unlikely that there was a mistake in the count of the number of supralabials. In our specimen the tail is only partially colored white or cream, not "entirely white." Hallowell mentions

no white on the tail of the type! If these are not anomalies one suspects the possibility that the specimens referred to this name by authors subsequent to Boulenger, have applied the name to a snake different from the type of *corpulentum*. Our specimen agrees in most characters with the form redescribed by Boulenger. The second labials are fused to the chinshields leaving the combined scale bordering the lip. There are five supralabials but there are 23 scalerows such as one expects on *leucura*.

Causus rhombeatus (Lichtenstein)

Sepedon rhombeatus Lichtenstein, Verz. Doubl. Mus. Berlin, 1823, p. 106 (type locality, Gold Coast)

Causus rhombeatus Boulenger, Proc. Zool. Soc. London, 1919, pts. 3 & 4, (Feb. 1920), p. 295, text fig. 1; Barbour and Loveridge, in Strong, Cont. Dept. Trop. Med. Inst. Trop. Biol. Med., No. 5, vol. 2, 1930, p. 774.

There are seven specimens in the collection: EHT-HMS Nos. 31881-31883; 31901-31904. The last four numbers are recently hatched individuals or (one) still in the egg.

The following data are taken from EHT-HMS No. 31881: Nostril wider than high, the part visible above forming a sharp angle separating the nasals and partially wedged between the internasals; internasals longer than the prefrontals, with a narrow posterior section that extends behind nasal, and is in contact with the loreal; prefrontals much wider than long; frontal subhexagonal, the sides parallel, longer than its distance to the tip of snout, longer than the parietals; nasal scale with a transverse arm separated from its fellow by the rostral, the large nostril pierced in the larger posterior part; the internasal forms a slight overhanging shelf above edge of nasal; loreal somewhat triangular; a single preocular (on one side partially sutured); supraoculars nearly as wide anteriorly as posteriorly; one postocular in contact with an elongate post-subocular, this scale with two other suboculars form a series that separates the labials from the orbit; supralabials, 6-6; infralabials, 9-9, four touching first chinshields; the second pair of chinshields not differentiated. Scales of the eleven median rows with a well-defined keel that does not extend the whole length of the scale; scale rows, 19-19-13: temporals, 2 + 3; ventrals, 125; anal single; subcaudals, 22, the last three undivided.

A large triangular or chevron-shaped black mark reaching to anterior edge of frontal; a dark indefinite line from eye to jaw angle; on neck there are chevron-shaped spots, white throughout most of body the median spots larger, somewhat rhomboidal with a lateral indefinite series of spots on the outer scalerows; whitish on chin and

throat; most of venter lavender gray-brown the pigment forming transverse markings on each ventral; area in front of vent much lighter than elsewhere on venter but with some dark flecks; sub-caudal area immaculate; tail above with a median black line.

Data on Causus rhombeatus Lichtenstein

Number	Sex	Ventrals	Sub-caudals	Total length	Tail	Scale formula
31881	♀	125	22	460	42	19, 19(18), 12(13)
31882	♂	125	22	397	41	19, 19, 11
31883	♂	127	23	405	38	19, 18(19), 13

Variation: The subcaudals for the most part are divided but No. 31881 has three, 31882 four and 31883 five of the terminal subcaudals undivided. The suboculars two or three. The infralabials touching the first chinshields are either four or five.

Remarks: Boulenger gives the range of ventrals as 120-155. Liberian specimens have a low number (125-127) while the highest counts occur much farther to the southeast.

"This is the commonest snake here on the plantation. It is called the 'yard snake' by the house servants, because they are so often found under the houses or in the yard close by. The men engaged in clearing operations report them as numerous in the low cut-over bush of old native farms. The engineer clearing a site for a new servants' camp behind the hospital compound complained one noon that he had killed eleven of them that morning.

"I have read that this species is the greatest cause of death by snake bite in the Nairobi area, but certainly here, although common, it does not cause as many deaths as *Naja melanoleuca*, or more especially, *Bitis gabonica*. It does not behave viciously, and the white children playing in the yards often find them and call the servants to kill them."

Bitis gabonica Duméril, Bibron and Duméril

Echidna gabonica Duméril, Bibron and Duméril, *Erpétologie générale*, vol. 7, pp. 1428-1430, pl. 80 bis (type locality, Côte du Gabon).

Heads from two large specimens (EHT-HMS Nos. 31899-31900) and two smaller complete specimens are from Harbel, Liberia. The two latter yield the following data respectively: Ventrals, 129, 131; subcaudals, 32, 28; anal single; supralabials, 14 (15), 14; scale-rows at middle of body, 36, 38; total length in mm., 395, 748; tail length, 36, 46.

"This is the snake that everyone here fears—an insolent vicious animal. They are common, four medium to large ones have been

found on the lawn at our house since we came here two years ago. Those of us with small children have to think of them constantly. They are beautifully colored yet seem to be easily overlooked on a green lawn. I send a color photograph of a specimen just killed on my driveway, but unfortunately the colors appear mostly tans and browns. In life, the reddish tan markings of preserved specimens, often, though not always, have a purplish-rose cast, whereas the areas that are gray in preservative are a rich powder-blue. The tan flush under the jaw is blood-colored in life, in fact on my first specimen seen, I thought the jaw was smeared with blood.

"Our soil here is laterite—a reddish soil and the young specimen I send was just that color. The varied markings of course were present but the general coloration was that of the soil, and since the soil is gravelly the markings correspond well to the shadows caused by the small gravel, and the snake was difficult to discern."

Bitis nasicornis (Shaw)

Coluber nasicornis Shaw, Nat. Misc. vol. 3, pl. 94 (type locality, "interior of Africa").

Two specimens, EHT-HMS Nos. 31896 ♀ - 31897 ♀ yield the following data respectively: Ventrals, 122, 127½; subcaudals, 27, 28; anals, single; supralabials, 15 (16), 15 (16); scalerows at middle of body, 35, 33; total length in mm., 530, 676; tail, 71-94.

"This species is also common along and in the waterways, but although I have been given a number of smaller specimens I have never yet seen one that approaches in size the medium-sized Gaboon viper. I presume they eat fish, at least sometimes, at any rate, since two of my specimens have been taken from the natives' fish traps, where they had drowned.

"This species is even more brilliant than *gabonicus*. The dark triangle on the head, however, is always black or dark brown, not reddish as it is sometimes depicted. I doubt that *Bitis arietans* occurs here in the rain forest."

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The Tetranychidae of Mexico (Acarina)

BY

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ABSTRACT. Mites of the family Tetranychidae known to occur in Mexico are included in this report. Twenty-five species distributed in seven genera are included, among which are ten previously named species reported for the first time from Mexico and eight species new to science. The eight new species are assigned to genera as follows: *Aplonobia*, two new species; *Neotetranychus*, four new species; *Eotetranychus*, one new species; *Oligonychus*, one new species.

Portions of this study were made possible through grants from the Greater University Fund, University of Kansas, which provided funds to finance surveys in Mexico during 1955 and 1956. The report on this project has been divided into sections, the first section, here presented, being restricted to mites of the family Tetranychidae.

It is undoubtedly true that the additional records of known species of tetranychid mites plus the new species described from collections made in Mexico in connection with this study represent a very small increment of the total number of species of mites in this family that occur in Mexico. The acarine fauna of Mexico has been virtually ignored by most collectors, or if not ignored then collections have been retired to some inaccessible recess where they will remain until renewed interest in this group of arthropods develops. It is hoped that this paper will contribute in a small way to the arousal of this interest in Mexican tetranychid mites and will stimulate field workers in Mexico to collect more assiduously the mites of this and other acarine families. It will be efforts of this sort that will ultimately provide the types of fundamental informa-

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tion necessary for the solution of complex problems in speciation, distribution and the like that will result in a better understanding of the relationships existing in the world fauna within the order Acarina. The importance of tetranychid mites to agriculture increases the urgency for discovering these relationships, for it is probably true that many forms as yet undescribed pose serious threats to areas of intensified and specialized crop production.

FAMILY TETRANYCHIDAE Donnadieu

The family Tetranychidae can be readily recognized by having the basal segments of the chelicerae fused to form a mandibular plate or stylophore. The stylophore therefore embraces the two recurved bases of the movable styletlike chelicerae which are long and slender appendages adapted for piercing. The fourth segment of the palpus bears a prominent claw situated dorsally at the distal end of the segment. The palpal tarsus, displaced to a ventral position by the tibial claw, provides a chelate arrangement of these terminal elements of the appendage often referred to as the "thumb-claw" process. There are not more than sixteen pairs of dorsal body setae. Tarsus I usually has two pairs of duplex setae and tarsus II bears a single pair.

Immediately following is a key to the genera of the family Tetranychidae now definitely known to be represented by species in Mexico. Since excellent keys are now available in the comprehensive work of Pritchard and Baker (1955), the present authors feel that this simplification of the key, which excludes several genera that may subsequently be collected in Mexico, is justifiable.

KEY TO GENERA KNOWN TO OCCUR IN MEXICO

1. Empodium bearing tenent hairs; duplex setae at extreme end of tarsus; female with three pairs of anal setae, male with five pairs of anal setae 2
 Empodium lacking tenent hairs; female with two pairs of anal setae, male with four pairs 3
2. Four pairs of dorsal propodosomal setae present; true claws long and well developed *Bryobia*
 Three pairs of dorsal propodosomal setae present; true claws absent, ... *Aplonobia*
3. Tarsus I empodium rudimentary; less than two pairs of duplex setae present *Eutetranychus*
 Tarsus I empodium well developed; two pairs of duplex setae present . . . 4
4. Two pairs of para-anal setae present; peritreme usually ends in a simple bulb 5
 One pair of para-anal setae present; peritreme usually ends in a chambered hook 6

5. Empodium divided on distal two thirds into three pairs of hairs, except leg I and II of male *Eotetranychus*
Empodium not divided on at least the proximal one half, ... *Neotetranychus*
6. Empodium with distal end divided into three pairs of hairs, *Tetranychus*
Distal end of empodium clawlike not divided, empodial claw subtended proximoventrally by numerous hairs *Oligonychus*

Genus BRYOBIA Koch

The genus *Bryobia* is distinctive in possessing four pairs of dorsal propodosomal setae. The true claws are well developed with lateral tenent hairs and they are usually retrorse on the distal end. The peritreme usually ends in an elongated chamber or an anastomosing enlargement.

Bryobia bakeri (McGregor)

The type specimens of this species were collected from Mt. Popocatepetl near Mexico (City) at 12,000 feet elevation from the trunk of a pine tree. A single female was collected in Texas by R. K. Fletcher on wheat.

Bryobia praetiosa Koch

Reported records of *Bryobia praetiosa* indicate that it is widely distributed throughout the world. The following collections are from Mexico: 9 miles east of Huezotzingo, Puebla, June 27, 1955, R. E. Beer and D. S. Lang, under rocks; 6 miles south of Avila Camacho, Puebla, June 29, 1955, R. E. Beer and D. S. Lang, under rocks; 7 miles northwest of León, Guanajuato, August 19, 1954, W. T. Atyeo, under rocks.

Genus APLONOBIA Womersley

The genus *Aplonobia* has the true claws reduced to slender pads bearing a pair of tenent hairs distally and the empodium consists of a slender pad with ventrally directed tenent hairs. There are only three pairs of dorsal propodosomal setae present. The termination of the peritreme is variable. The inner sacral setae are in line with the dorsocentral setae and resemble a fourth pair of dorsocentrals.

Aplonobia verrucosa sp. nov.

(Figs. 2, 3, 4, 5)

Female: Terminal sensillum of palpus longer than claw, slender, spinelike; dorsal fusiform setae slender, half as long as sensillum. Stylophore about as long as broad, emarginate on posterior border, striations longitudinal; peritreme strongly elbowed, ending in enlarged branched leaflike chamber. Tarsus I with three ventral tactile setae proximal to duplex setae, proximal member of duplex setae

minute; tibia I with four tactile and three sensory setae. Tarsus II with three ventral tactile setae proximal to duplex setae; tibia II with four tactile and two sensory setae. First and fourth pairs of legs longer than legs II and III, legs of uniform thickness to end of tarsus, abruptly angled at union of empodium; empodium on slender pedicel. First pair of dorsal propodosomal setae half as long as other setae, slightly petiolate, plumose; remainder of dorsal setae uniformly tapering to point, much longer than interval separating them, set on strong tubercles. Humeral setae absent. Integumentary striae transverse on propodosoma, longitudinal in areas of hysterosomal and sacral setae. Body thrown into numerous folds. Length of body 420 μ , including rostrum 505 μ ; greatest width of body 340 μ .

Male: Similar to female. First pair of legs longer than other legs. Aedeagus long, gently undulating, leveling slightly dorsad, broadest at base, distal end abruptly tapering to rounded tip. Length of body 412 μ , including rostrum 500 μ .

In life the females are green with yellowish legs and males are yellow with legs pink or orange near their apices. Although quite abundant on the host plants in the area, they were scattered on both surfaces of the leaves indicating an absence of the gregarious habit. Webbing was absent. Mites were present in equal numbers on old and new foliage. No eggs were seen though they were probably abundant but concealed beneath the dense pubescence of the under leaf surfaces. Several males were assembled around most of the molting, quiescent females.

Holotype: Male, 10 miles south of Chila, Oaxaca, Mexico, July 6, 1956, R. E. Beer, on *Lippia graveolens*.

Allotype: Female, same data as holotype.

Paratypes: Several males and females with same data as holotype.

Location of types: Holotype, allotype and several paratypes of both sexes in the Snow Entomological Museum, University of Kansas. Four males and four females (paratypes) deposited in the United States National Museum.

Aplonobia dyschima sp. nov.

(Figs. 3, 6)

Female: Terminal sensillum of palpus thin, setalike. Stylophore with longitudinal striae; peritremes protruding anteriorly, elbowed, enlarged anastomosing chambers at distal ends. Duplex setae on tarsus I adjacent, proximal member short, less than one fourth as long as distal member; four plumose tactile setae on dorsal surface,

eight tactile and one sensory setae on ventral surface proximal to duplex setae; tibia I with six plumose tactile setae and one simple sensory seta on dorsal surface. Five plumose tactile setae on ventral surface. Tarsus II with proximal member of duplex setae plumose, one third as long as distal member, four plumose tactile setae and three sensory setae proximal to duplex setae; tibia II with seven plumose tactile setae. Empodium of all legs longer than pad of true claw. First pair of dorsal propodosomal setae lanceolate, longer than other dorsal setae which are spatulate. Striations fine, transverse; surface of body thrown into folds. Length of body 495 μ , including rostrum 555 μ ; greatest width 410 μ .

Male: Unknown.

Holotype: Female, General Terán, Nuevo León, Mexico, July 19, 1954, W. T. Atyeo, on *Acacia* sp.

Paratypes: Several females, same data as holotype.

Location of types: Holotype and several paratypes in Snow Entomological Museum, University of Kansas. Two paratypes deposited in the United States National Museum.

Aplonobia dyschima resembles *Monoceronychus corynetes* in having subspatulate dorsal setae and in the general body shape but can be separated by the length of the front legs. *M. corynetes* has the front pair of legs one and one-half times as long as the body while the legs of the first pair of *A. dyschima* are approximately as long as the body. Further separation is by the duplex setae on tarsus I, *A. dyschima* has the proximal member plumose and one-third as long as the distal member.

Pritchard and Baker (1955) state that *M. corynetes* is intermediate between *Aplonobia* and *Monoceronychus* due to the round body and in lacking a propodosomal projection, but these authors in a recent consultation have indicated that a transferral of *M. corynetes* to the genus *Aplonobia* is forthcoming in a future publication. *Aplonobia* is similar to *M. corynetes* in the position of the inner sacral setae, general body shape and in the degree of the propodosomal modification. However, because of the submedian position of the inner sacrals, the absence of an anterior dorsal projection of the propodosoma and the presence of a single rather than two dorsal shields serve to separate both *M. corynetes* and *A. dyschima* from the typical *Monoceronychus*. In Pritchard and Baker's key *A. dyschima* will run to *A. myops* but differs from this species in dorsal setation and other characters. The future discovery of additional species of *Aplonobia* and *Monoceronychus* may provide a better understanding and delineation of the genera.

Genus *EUTETRANYCHUS* Banks

The genus *Eutetranychus* can be recognized by lacking the two pairs of duplex setae on tarsus I and II. A single pair of associated setae, resembling duplex setae, is often present. The empodium is greatly reduced and appears absent and the true claws are reduced to short pads with a pair of distally directed tenent hairs.

Eutetranychus banksi (McGregor)

This mite is apparently widely distributed, being reported from North, Central and South America, Europe, Africa and Asia. Its host associations are numerous with no significant plant relationships indicated. The following collections from Mexico are here recorded: El Salto Falls, San Luis Potosí, Mexico (*Citrus* sp.); 6 miles west of Teziutlán, Puebla, Mexico (orange); 16 miles north of Juchitan, Oaxaca, Mexico (*Vatairea Lundellii*). In life, females are brownish and males reddish-brown. They inhabit the upper surfaces of the leaves. No webbing is produced.

Genus *NEOTETRANYCHUS* Trägårdh

The genus *Neotetranychus* is distinctive in having the single empodial claw well developed and undivided on at least the proximal half. There are two pairs of para-anal setae present and the peritreme usually ends in a simple bulb.

As an aid to the identification of the known species of the genus, a complete key to species of *Neotetranychus* follows. This key includes several species not now known to occur in Mexico.

KEY TO THE SPECIES OF *NEOTETRANYCHUS*

- | | |
|---|----------------------|
| 1. Body with dorsal setae longer than longitudinal interval separating adjacent setae | 2 |
| Body with dorsal setae shorter than longitudinal interval separating adjacent setae | 5 |
| 2. Dorsal setae set on tubercles | 3 |
| Dorsal setae not set on tubercles | 4 |
| 3. Tibia II with seven tactile setae (Europe) | <i>rubi</i> |
| Tibia II with six tactile setae | <i>siccus</i> |
| 4. Empodium with three pairs of hairs at distal end | <i>undulatus</i> |
| Empodium simply clawlike | <i>hamus</i> |
| 5. Empodium with three pairs of hairs at distal end | <i>virginiensis</i> |
| Empodium simply clawlike | 6 |
| 6. Dorsocentral hysterosomal setae slender, shorter than the longitudinal interval between adjacent setae | <i>hakea</i> |
| Dorsocentral hysterosomal setae not slender | 7 |
| 7. Dorsal setae leaflike | <i>flabellosetus</i> |
| Dorsal setae oblong spatulate | <i>hispidosetus</i> |

Neotetranychus hispidosetus sp. nov.

(Figs. 1, 3, 4)

Female: Terminal sensillum of palpus two and one-half times as long as broad; fusiform setae slender, longer than sensillum. Stylophore about as broad as long, strongly emarginate on posterior border, striations longitudinal; peritreme straight distally ending in simple bulb. First and third pairs of dorsal propodosomal setae longer than interval separating adjacent setae, second pair much shorter, broader and rounder at tip; inner sacral setae small, spatulate, outer sacral setae twice as long, swollen at tip. Integumentary striae beadlike, irregular, longitudinal in area of dorsal propodosomal setae, transverse in area of dorsocentral hysterosomal setae, transverse in area of sacral setae. Tarsus I with duplex setae adjacent, proximal member small, four tactile and three sensory setae proximal to duplex setae; tibia I with seven tactile and two sensory setae. Tarsus II with two tactile and one sensory seta proximal to duplex setae; tibia II with four tactile and two sensory setae. Length of body 480 μ , including rostrum 560 μ ; greatest width 316 μ .

Male: Similar to female. Terminal sensillum of palpus minute; dorsal fusiform setae slender, long. Sacral setae all similar in length and shape. Leg I approximately as long as body; tarsus I with four tactile and three sensory setae proximal to duplex setae; tibia I with nine tactile and two sensory setae. Tibia II with five tactile setae. Aedeagus gently curves dorsad, ending in compact enlargement, ventral angles approximately equal. Length of body 390 μ , including rostrum 430 μ .

Holotype: Male, 17 miles north of Tehuiztingo, Puebla, Mexico, July 17, 1955, R. E. Beer and D. S. Lang on *Erythrina* sp.

Allotype: Female, same data as holotype.

Paratypes: Several males and females with same data as holotype.

Location of types: Holotype, allotype and several paratypes of both sexes located in the Snow Entomological Museum, University of Kansas. Five males and one female (paratypes) deposited in the United States National Museum.

This species is pale yellow and slightly speckled with brown in life. The types were collected from a very large population of mites that was present in equal numbers on both surfaces of the leaves of the host plant (coral tree). Eggs were pale yellow and spheroid, webbing sparse. Damage to the host plant was severe.

Neotetranychus hamus sp. nov.

(Figs. 1, 4)

Female: Terminal sensillum of palpus large, three times as long as broad; dorsal fusiform setae slender, oblong. Stylophore one and one-half times as long as broad, strongly emarginate on posterior border; peritreme straight distally ending in simple bulb. Leg I slightly longer than other legs; tarsus I with four tactile setae proximal to duplex setae, proximal member of duplex setae half as long as distal member; tibia I with eight tactile and two sensory setae. Tarsus II with proximal member of duplex setae half as long as distal member; tibia II with six tactile setae. Empodium of all legs similar. Dorsal setae of body petiolate, pubescent, slightly expanded near base, tapering to point, about as long as longitudinal interval separating them. Integumentary striae transverse. Length of body 300μ , including rostrum 370μ ; greatest width of body 228μ .

Male: Similar to female. Terminal sensillum of palpus minute, dorsal fusiform setae long, slender. Tarsus I with three tactile and two sensory setae proximal to duplex setae; proximal member of duplex setae half as long as distal member; tibia I with seven tactile and two sensory setae. Tibia II with six tactile setae. Aedeagus bends dorsad, corniform, one and one-half times as long as broad, tapering abruptly from base to pointed apex. Length of body 290μ , including rostrum 340μ .

Holotype: Male, 5 miles north of Tepic, Nayarit, Mexico, July 26, 1956, R. E. Beer.

Allotype: Female, same data as holotype.

Paratypes: Several males and females with same data as holotype.

Location of types: Holotype, allotype and several paratypes of both sexes deposited in the Snow Entomological Museum, University of Kansas. Two males and two females (paratypes) deposited in the United States National Museum.

This species differs from *N. siccus* in length of members of duplex setae, dorsal setation not being set on tubercles, and terminal sensillum of palpus being broad. Aedeagus is most similar to *N. rubi* but is not as slender nor as pointed and large; not sickle-shaped as in *N. rubi*.

In life this mite is elongate and greenish-yellow in color. Eggs are pale yellowish and spheroid. Webbing was not apparent in live colonies. The identity of the host plant is not known but field notes indicate that it was a woody shrub or tree with trifoliolate leaves (Leguminosae?). Damage to the host was moderately severe.

Neotetranychus flabellosetus sp. nov.

(Figs. 1, 3, 4)

Female: Terminal sensillum of palpus two and one-half times as long as broad, uniform diameter on proximal two thirds, tapers to angulate tip on distal one third. Stylophore twice as long as broad, emarginate on posterior border, broadly rounded on anterior margin; peritreme ends in a simple bulb. Tarsus I with duplex setae adjacent, proximal member of duplex setae small, less than one-fourth as long as distal member, five tactile setae proximal to duplex setae; tibia I with seven tactile and two sensory setae. Tarsus II with proximal member of duplex setae one-third as long as distal member, three tactile and one sensory setae proximal to duplex setae; tibia II with six tactile setae. Empodium of all legs simply clawlike. First pair of dorsal propodosomal setae over twice as long as other propodosomal setae, clunal setae similar to first pair of propodosomal setae, remaining dorsal setae short, spatulate, plumose. Integumentary striae transverse except for longitudinal striae in area of sacral setae. Length of body 450 μ , including rostrum 505 μ ; greatest width of body 324 μ .

Male: Similar to female. Tarsus I with six tactile setae proximal to duplex setae; tibia I with seven tactile and four sensory setae. Aedeagus broad at base, curving slightly dorsad, terminating on distal end in an angulated enlargement, dorsal and ventral angulations approximately equal. Length of body 300 μ , including rostrum 380 μ .

Holotype: Male, 16 miles north of Juchitan, Oaxaca, Mexico, July 13, 1955, R. E. Beer and D. S. Lang, on *Cassia bacillaris*.

Allotype: Female, same data as holotype.

Paratype: One female, same data as holotype.

Location of types: Holotype, allotype and paratype in the Snow Entomological Museum, University of Kansas.

The male of *Neotetranychus flabellosetus* resembles *N. virginien-sis* and *N. hispidosetus* in the appearance of the aedeagus, *N. virginien-sis* can be recognized by having the empodium divided into three pairs of hairs. *N. hispidosetus* can be separated from *N. flabellosetus* by the dorsal setation, *N. flabellosetus* has short, spatulate setae on the dorsum while *N. hispidosetus* has oblong, spatulate setae.

Neotetranychus undulatus sp. nov.

(Figs. 1, 4)

Female: Terminal sensillum of palpus two and one-half times as long as broad; dorsal fusiform setae broad, ovate. Stylophore broadly rounded, approximately two times as long as broad, emar-

ginate on posterior margin, with longitudinal striations. Peritreme straight proximally, bent distally to form an elongated chamber. Tarsus I with five tactile setae proximal to duplex setae, proximal member of duplex setae small, one-fourth as long as distal member; tibia I with seven tactile and two sensory setae. Tarsus II with proximal member of duplex setae one-fourth as long as distal member, three tactile and one sensory setae proximal to duplex setae; tibia II with six tactile setae. Dorsal setae of body slender, about as long as longitudinal interval separating them. Integumentary striae transverse except for longitudinal striations in area of sacral setae. Length of body 560μ , including rostrum 600μ ; greatest width of body 380μ .

Male: Similar to female. Integumentary striae transverse. Tarsus I with proximal member of duplex setae one-half as long as distal member, three tactile setae and two sensory setae proximal to duplex setae; tibia I with nine tactile and two sensory setae. Tibia II with seven tactile and two sensory setae. Aedeagus long and slender, strongly undulate, tapering to rounded tip. Length of body 420μ , including rostrum 540μ .

Holotype: Male, two miles west of Antiguo Morelos, Tamaulipas, Mexico, August 3, 1955, R. E. Beer and D. S. Lang, on *Beaucarnea stricta*.

Allotype: Female same data as holotype.

Paratypes: Two females, same data as holotype.

Location of types: Holotype, allotype and one paratype in the Snow Entomological Museum, University of Kansas. One paratype deposited in the United States National Museum.

In life, mites of this species are pale yellow in color. They assemble in small colonies on the under sides of the slender leaves of the host plant. Eggs are pale yellow and spheroid and webbing is sparse. (Author's note: A large collection taken in the type locality in 1956 was lost in transit.)

Genus EOTETRANYCHUS Oudemans

The genus *Eotetranychus* possesses two pairs of para-anal setae. The duplex setae on tarsus I are adjacent and the legs tend to terminate abruptly. The empodium consists of three pairs of distally directed hairs and the peritreme usually ends in a simple bulb.

Eotetranychus oistus sp. nov.

(Figs. 2, 4)

Female: Terminal sensillum of palpus twice as long as broad, dorsal fusiform setae slender, about as long as terminal sensillum. Stylophore one and one-half times as long as broad, emarginate on posterior border, abruptly rounded on anterior border; peritreme straight distally ending in simple bulb. Tarsus I with four tactile setae proximal to duplex setae, proximal member of duplex setae one-fourth as long as distal member; tibia I with six tactile and four sensory setae. Tarsus II with four tactile setae proximal to duplex setae; tibia II with eight tactile setae. Dorsal body setae gently tapering to a point, longer than interval separating adjacent setae; dorsal striations transverse. Length of body 390μ including rostrum 450μ ; greatest width of body 250μ .

Male: Similar to female. Terminal sensillum of palpus minute, appearing absent. Tarsus I with four tactile and two sensory setae proximal to duplex setae. Tarsus II with three tactile and one short sensory setae proximal to duplex setae. All legs short and stubby. Aedeagus small, twice as long as broad, dorsal surface with indentation, tapering abruptly to a point, ventral surface uniformly tapering to tip. Length of body 300μ , including rostrum 380μ .

Holotype: Male, Atlixco, Puebla, Mexico, July 19, 1955, R. E. Beer and D. S. Lang, on *Ipomoea arborescens*.

Allotype: Female, same data as holotype.

Paratypes: Several males and females with same data as holotype.

Location of types: Holotype, allotype and several paratypes of both sexes located in the Snow Entomological Museum, University of Kansas. Two males and one female (paratypes) in the United States National Museum.

Eotetranychus oistus belongs to the Tiliarum Group of Pritchard and Baker. It resembles *E. malvestris* but can be separated easily by differences in the aedeagi. Tight colonies were present along the mid-vein of the leaf on the under surface. The mites were yellow in life, eggs spheroid and webbing sparse. Damage to the leaves of the host plant was severe.

Eotetranychus deflexus (McGregor)

This species has heretofore been reported only from California and Oregon with the only recorded host, snowberry (Oregon). The following collections are now recorded: 19 miles north of Huachi-

nango, Puebla, Mexico (blackberry); 12 miles west of Huachinango, Hidalgo, Mexico (*Quercus crassifolia*). Mites are yellowish in life and form dense colonies on the under surfaces of the leaves of the host plant. Webbing is dense, eggs pale and spheroid. Damage to blackberry was severe but only negligible on *Quercus*.

Eotetranychus carpini (Oudemans)

Pritchard and Baker have indicated subspeciation in this species as an answer to variability in certain morphological characters that is correlated with distribution. According to their proposed groupings, the following collections based upon the morphological distinctions they suggest, are recorded for *E. carpini carpini*: México (city), D. F. Mexico, (cottonwood and sycamore); 19 miles north of Huachinango, Puebla, Mexico (alder); 4 miles south of Teziutlán, Puebla, Mexico (alder). The subspecies *carpini* has heretofore been regarded as restricted to the Old World, with *borealis* occurring in western North America. This Mexican record for *carpini* therefore represents a significant distribution record, in extending *carpini* into the Western Hemisphere. Mites from the above Mexican collections were in each case inflicting serious damage upon the host plants. Colonies are formed on the under sides of leaves. Eggs are pale and spheroid and webbing abundant. Live mites are yellow in color. Previous host records from Canada, Europe and the United States indicate a restriction to deciduous trees, shrubs and brambles which is compatible with observations on the Mexican collections here recorded.

Eotetranychus steganus Pritchard and Baker

This species has previously been known from a single area, Florida, and its host associations restricted to a single plant group, palmetto. A second collection is here recorded as follows: El Salto Falls, San Luis Potosí, Mexico (*Sabal mexicana*).

Eotetranychus ecclisis Pritchard and Baker

This species is known from a single host species, *Artemisia mexicana*, and at the present time the known distribution is restricted to the type collection data as follows: Mexico (city)—Cuernavaca Highway, kilometer 67, January 22, 1941, E. W. Baker.

Eotetranychus perplexus (McGregor)

This species is recorded from California and Idaho on *Cercocarpus*, from California on *Salix*, from Washington on *Prunus emarginatus*, and from British Columbia, California and Washington on *Purshia*. The following distribution and host record is added at

this time: 17 miles north of Tehuitzingo, Puebla, Mexico, July 18, 1955, R. E. Beer and D. S. Lang, on *Cryptocarpa procera*. In life these mites were small and yellowish. They assembled in small, tight colonies on the lower surfaces of the leaves. Eggs were pale yellowish and webbing abundant.

In the Mexican collection the male aedeagus deviates slightly from the configuration ordinarily associated with the species, in being bent more strongly ventrad just before its apex. However, this difference is not considered to represent more than that which would be expected in comparing specimens varying in appearance because of orientation on the slide.

Genus OLIGONYCHUS Berlese

The genus *Oligonychus* has the empodium divided into several hairs proximoventrally and hooklike on the distal end. A single pair of para-anal setae is present and the dorsal setae are not set on tubercles.

Oligonychus flexuosus sp. nov.

(Figs. 2, 3, 4)

Male: Terminal sensillum of palpus pronounced, more than twice as long as broad; dorsal fusiform setae nearly as long as sensillum. Stylophore broadly rounded anteriorly, slightly emarginate posteriorly, with longitudinal striae. Peritreme straight distally, ending in a simple bulb. Tibia I with nine tactile and one sensory setae; tarsus I with four tactile setae proximal to duplex setae; duplex setae widely spaced, proximal member short; empodium I split to form two stout curved claws. Tibia II with five tactile setae; tarsus II with four tactile setae proximal to duplex setae; tibia II with seven tactile setae. Dorsum of body with slender tapering setae, longer than the interval separating adjacent setae; dorsal striae transverse in area of histerosomals, longitudinal posterior to sacral setae. Four pairs of genitoanal setae present. Aedeagus broad at basal fifth, abruptly tapering to a uniformly slender shaft which curves dorsad; distal fifth broadly curving posteriorly. Length of body 305 μ , including rostrum 334 μ .

Female: Similar to male. Terminal sensillum of palpus shorter and broader than male, dorsal fusiform setae slightly longer than sensillum. Empodium I divided to form two claws, three pairs of empodial hairs below the empodial claws. Two pairs of anal setae present. Length of body 362 μ , including rostrum 411 μ ; greatest width of body 234 μ .

Holotype: Male, 10 miles south of Chiapa, Chiapas, Mexico, July 12, 1955, R. E. Beer and D. S. Lang, on wild grass (*Paspalum humboldtianum*).

Allotype: Female, same data as holotype.

Paratypes: Several males and females of both sexes, same data as holotype.

Location of types: Holotype, allotype and several paratypes in the Snow Entomological Museum, University of Kansas. Two males and two females deposited in the United States National Museum.

Oligonychus flexuosus belongs to the Pratensis Group of Pritchard and Baker. Members of this group can be recognized by empodium I of the male which is split into two claws, aedeagus bending dorsad, tibia I bearing nine tactile setae and tarsus I bearing four tactile setae. The peritreme ends in a simple bulb. The females of this group cannot be differentiated as to separate species. The male of *O. flexuosus* is readily recognized by the extremely long, slender aedeagus. Other members of the group have the distal end of the aedeagus sigmoid or with a compact enlargement, while the end of the aedeagus in *O. flexuosus* is simple. The aedeagus of *O. mcgregori* resembles *O. flexuosus* in having a slender prolongation but differs in having a strong barb at the base. In addition these species can be separated by the peritremes, *O. mcgregori* having a retrorse peritreme. Empodium I of *O. mcgregori* consists of three pairs of empodial hairs below the slender empodial claw, while *O. flexuosus* has empodium I divided into two claws.

In life both sexes were yellowish. The colonies were in tight clusters on the lower surface of the leaves. The leaves showed a yellow to brown discoloration in clearly defined patches embracing the area occupied by the colony. The eggs were pale and spheroid without a central stipe.

Oligonychus aceris (Shimer)

This species has been recorded from Indiana, Kansas, New Jersey, New York, North Carolina, Washington, and District of Columbia in the United States, with all recorded collections from maple. To this distribution and host record is added the following: El Salto Falls, San Luis Potosí, Mexico, August 1, 1955, R. E. Beer and D. S. Lang, on sycamore. Observations of the mites at the time the Mexican collections were made revealed that they assembled in small colonies on the upper surface of the leaf. Feeding caused a russet discoloration on the infested area. Adult mites were reddish-

brown with reddish shoulders and capitulum and pinkish legs. Eggs were pale yellow, circular in outline, flattened and had a central stipe. Webbing was present but not profuse.

Oligonychus propetes Pritchard and Baker

All previously recorded collections of this species were taken from oak in the eastern United States at the following locations: North Carolina, Virginia, District of Columbia. A collection from Mexico is here added to the known distribution records and may be identified by the following data: 6 miles north of Jacala, Hidalgo, Mexico, July 30, 1955, R. E. Beer and D. S. Lang, on *Quercus* sp. In life small colonies of the yellow mites were present on the under sides of the pubescent leaves and caused a yellowish discoloration of the dark, glossy, green upper surfaces of the leaves. Eggs were pale yellow.

Oligonychus stickneyi (McGregor)

Specimens of this species are recorded from Arizona, California, and Florida in the United States and from Morelos in Mexico. The U. S. collections were taken from various species of grass and from corn and maize. The Mexican collection was taken on maize. The following collection is here added to the Mexican distribution record: México (city), D. F. Mexico, June 22, 1956, R. E. Beer, on grass.

Oligonychus mcgregori (Baker and Pritchard)

This species has been known previously only by the type specimens which were taken from cotton at Chinandega, Nicaragua. It is here recorded for the first time from Mexico, this collection identified with the following data: 16 miles north of Juchitan, Oaxaca, Mexico, July 3, 1955, R. E. Beer and D. S. Lang, on *Vatairea Lundellii*. In life the mites are yellowish with brown spots, the dorsum is flattened. They cluster on the upper surfaces of the glossy leaves of the host plant along the mid-vein. Eggs are yellowish, circular in outline and flattened. Webbing is sparse. The mites were quite abundant and damage to the host conspicuous.

Oligonychus viridis (Banks)

This species is recorded from pecan in Florida, Georgia and Louisiana. Collections here reported from Mexico would indicate that it is generally distributed throughout the length of this country. The following localities and host records are added to the published information on *O. viridis*: El Salto Falls, San Luis Potosí, Mexico (avocado); México (city), D. F. Mexico, and Teziutlan,

Puebla, Mexico (camellia); 4 miles west of San Cristóbal de las Casas, Chiapas, Mexico (*Chimaphyla maculata*). Adult females in life are maroon or brownish with pale legs. They assemble in small, tight colonies with moderate webbing on both leaf surfaces. Damage to the host is a russet discoloration of the green leaves.

Genus *TETRANYCHUS* Dufour

The genus *Tetranychus* can be recognized by the single pair of para-anal setae and by having the duplex setae separated on tarsus I. The legs tend to taper to the empodium which is composed of three pairs of hairs. The peritreme usually ends in a chambered hook.

Tetranychus mexicanus (McGregor)

This species has been collected on citrus in the following localities: Laredo, Texas, Quarantine station, host (orange) shipment originating in Mexico; Monte Alto, Texas (lemon); Valles, San Luis Potosí, Mexico; Concordia, Argentina. To these distribution and host records may be added the following: 20 miles south of Acayucan, Veracruz, Mexico (wild banana); Tecolutla, Veracruz, Mexico (coconut palm). The following information concerning the Acayucan collection from banana was recorded in field notes: In life, female mites are robust and maroon in color with pink legs and gnathosoma; males are orange. Eggs are pale yellow and spheroid, webbing profuse, and dense colonies occur on the under sides of the leaves. The mites were exceedingly abundant and damage to the host severe. As regards the Tecolutla collection field notes indicate that in life, female mites are robust and red in color.

Tetranychus pacificus (McGregor)

This species is known from California, Idaho and Oregon where it has been reported from a multitude of hosts including several deciduous trees and shrubs, herbaceous annuals, melons and the like. To this distribution and host list may be added the following: 10 miles north of Matias Romero, Oaxaca, Mexico (*Asarum* sp.); El Salto Falls, San Luis Potosí, Mexico (*Bacconia frutescens*). In both of the Mexican collections, living mites were scattered on the leaves of the host plants and populations small. It would seem that the scarcity of individuals would mask a true gregarious habit if such were the case with this species.

Tetranychus telarius (Linnaeus)

The following locality and hosts are added to the exceedingly long lists of similar information for this species: Mexico (city), D. F. Mexico, (*Fraxinus* sp. and *Convolvulus* sp.). Damage to each of these hosts, ash planted as street trees and wild *Convolvulus* weeds was very severe. In the *Fraxinus* collections the live mites were the typical yellowish color phase. In the *Convolvulus* collections the living mites were maroon in color.

Tetranychus dugesii Cano and Alcacio

As suggested by Pritchard and Baker (1955) this species is at present under questionable assignment to the genus *Tetranychus*. Type material is identified with the following information, though the location of the type specimens is not known: Hacienda Escuela, México, on *Medicago denticulata*. This is the only known reference to this species.

The authors owe a debt of gratitude to several botanists who gave generously of their time and energy to assist with host identifications. We wish to express our thanks to Eizi Matuda and Faustino Miranda of the Instituto Biológico in México (city) and to W. H. Horr of the University of Kansas.

REFERENCES CITED

PRITCHARD, A. EARL, and BAKER, EDWARD W.

1955. A Revision of the Spider Mite Family Tetranychidae. Pacific Coast Entomological Society, Memoirs Series, vol. 2, 472 pp., 1955.

FIGURE 1

Figures in left column are female tibia and tarsus I. Figures in right column are female tibia and tarsus II. All magnifications are identical.

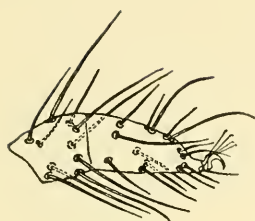
Neotetranychus hamus sp. nov.

N. hispidosetus sp. nov.

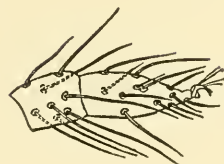
N. flabellosetus sp. nov.

N. undulatus sp. nov.

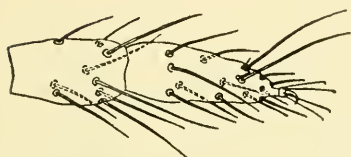
FIGURE 1



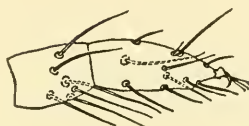
N. homus



N. hispidosetus



N. flabellosetus



N. undulatus

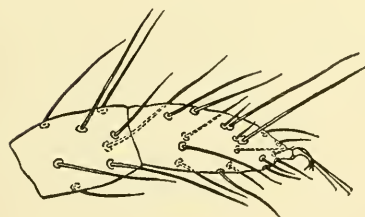


FIGURE 2

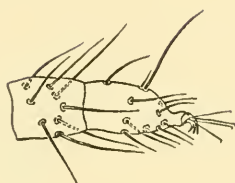
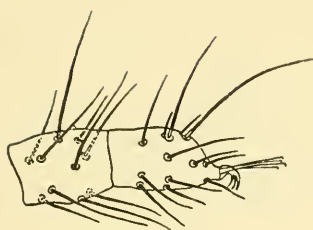
Figures in left column are female tibia and tarsus I. Figures in right column are female tibia and tarsus II. All magnifications are identical.

Eotetranychus oistus sp. nov.

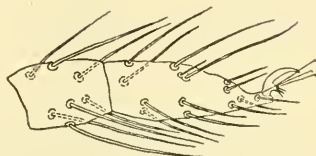
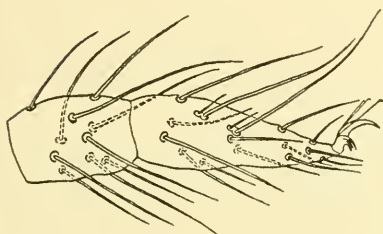
Oligonychus flexuosus sp. nov.

Aplonobia verrucosa sp. nov.

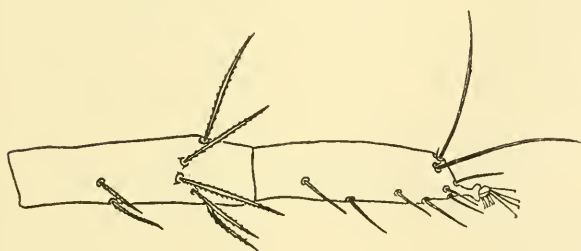
FIGURE 2



E. oistus



O. flexuosus



A. verrucoso

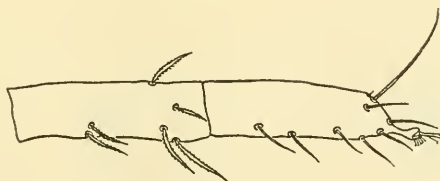


FIGURE 3

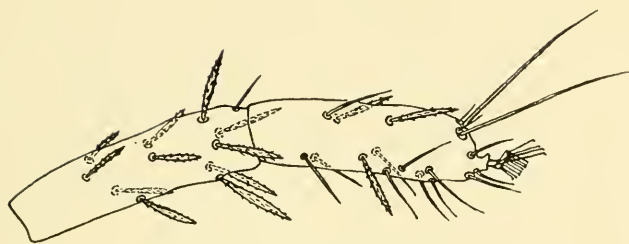
Tibia and tarsus I and II, *Aplonobia dyschima* sp. nov. Pretarsus of leg I of male, *Oligonychus flexuosus* sp. nov. Palpus of *Aplonobia verrucosa* sp. nov. Typical dorsocentral setae (identical magnification) of:

Neotetranychus hispidosetus sp. nov.

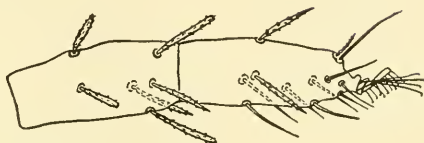
N. flabellosetus sp. nov.

Aplonobia dyschima sp. nov.

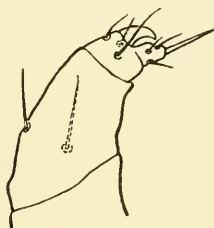
FIGURE 3



A. dyschima



Q. flexuosus



A. verrucosa



N. hispidosetus



N. flabellosetus



A. dyschima

FIGURE 4

Aedeagi of males (identical magnification):

Neotetranychus hamus sp. nov.

N. flabellosetus sp. nov.

N. hispidosetus sp. nov.

N. undulatus sp. nov.

Eotetranychus oistus sp. nov.

Oligonychus flexuosus sp. nov.

Aplonobia verrucosa sp. nov.

FIGURE 4



N. hamus



N. flabellosetus



N. hispidosetus



N. undulatus



E. oistus



O. flexuosus

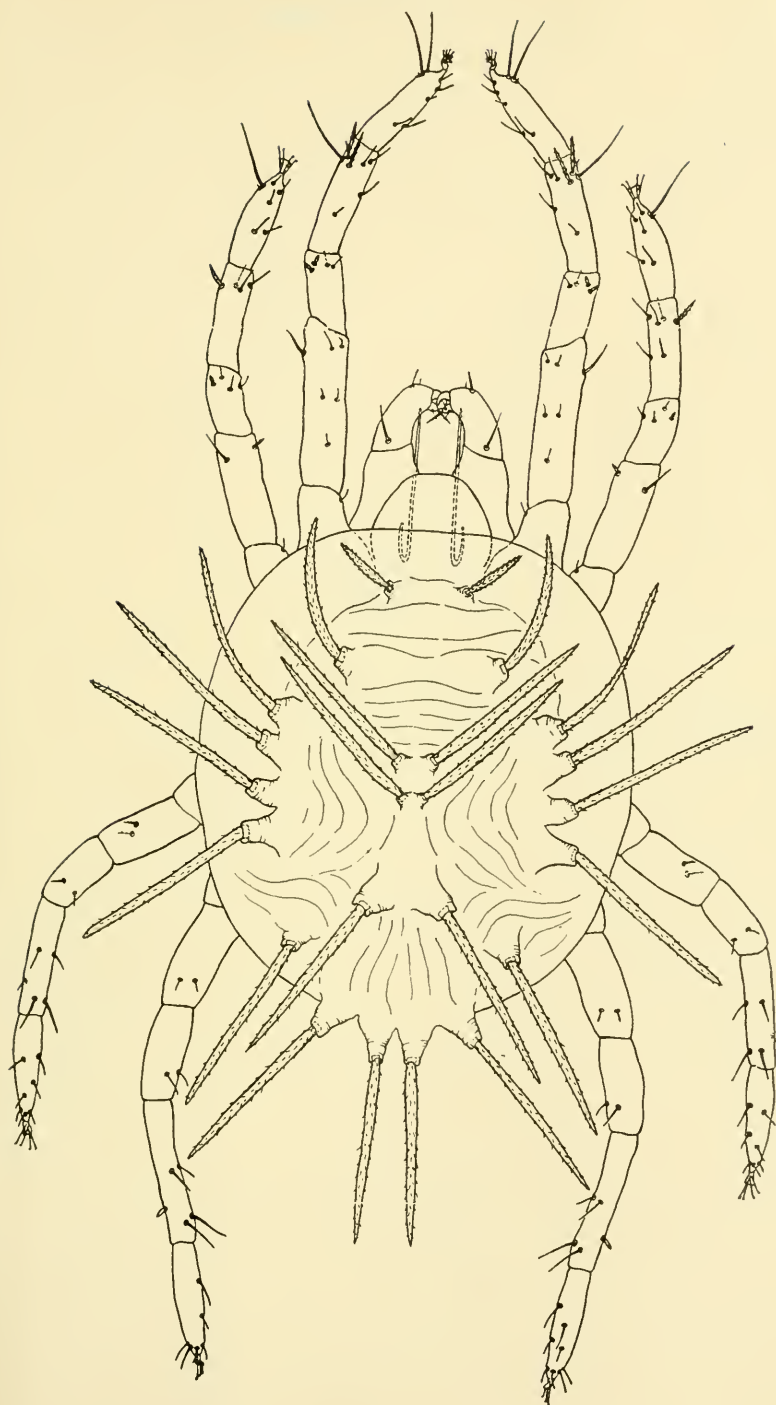


A. verrucosa

FIGURE 5

Adult female, *Aplonobia verrucosa* sp. nov. (dorsal aspect).

FIGURE 5

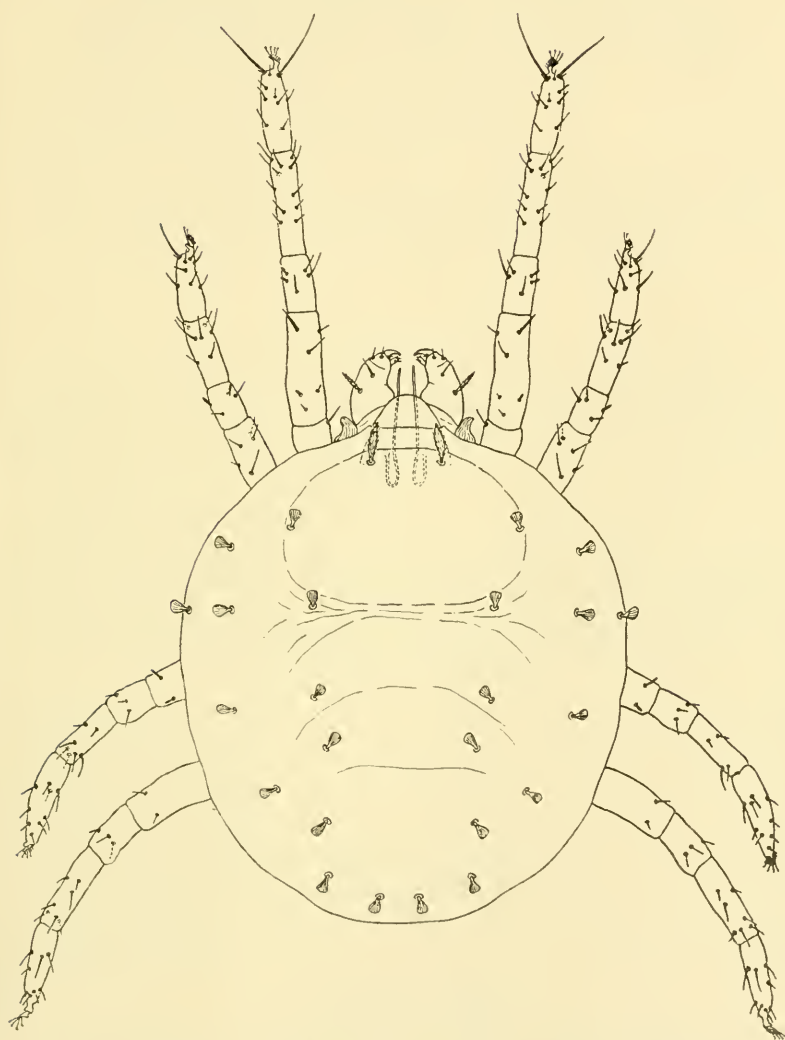


Apionobia verrucosa

FIGURE 6

Adult female, *Aplonobia dyschima* sp. nov. (dorsal aspect).

FIGURE 6



Apionobia dyschima

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[No. 16

A Revision of the Bees of the Subgenus *Epinomia* in the New World (Hymenoptera-Halictidae)*

BY

EARLE A. CROSS

ABSTRACT. This is the first of two papers dealing with the systematics and geographical variation of the New World members of the subgenus *Epinomia* Ashmead. It contains a revision of the subgenus and includes information on distribution, geographical variation, and flower preferences of its species. About 1500 specimens were examined.

Indications of the relationships between the subgenera of *Nomia* and a subgeneric key are presented.

Four species are recognized, one of which (*N. nevadensis*) is further divided into five subspecies. A more detailed study of the geographical variation of this species will be published elsewhere. Two species, *N. boharti* and *N. micheneri*, and one subspecies, *N. nevadensis stellata*, are described as new.

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INTRODUCTION

The purpose of this paper is to reclassify the species of the subgenus *Epinomia* and to give a brief survey of their variation. The subgenus is a small one, consisting of only four species, one of which (*N. nevadensis*) is divided here into five subspecies. From an

* Contribution number 957 from the Department of Entomology, University of Kansas.

evolutionary and systematic standpoint, however, the group is interesting since two of its species exhibit strikingly different forms. A more detailed study of the geographical variation within one species, *N. nevadensis*, will be published elsewhere.

Descriptions of new forms are based upon the type specimens, variation encountered within the type series being indicated in parentheses. The redescrptions of previously described forms are based upon series rather than single specimens. The author has followed the terminology utilized by Michener, 1944, for all descriptive purposes. The various processes of the apical margin of the clypeus referred to in the descriptions are obscure when viewed in facial aspect and are best seen from beneath.

Measurements of width and length of face were made as follows:

1. Greatest possible width of face, including eyes.
2. Greatest possible length of face, taken along sagittal plane.

The former was chosen for statistical treatment because it is measurable with a greater degree of accuracy than the other and because it is believed to be a good index of general size.

The first segment of the labial palpus was considered to consist only of the sclerotized portion of that segment, the conjunctiva between palpus and palpiger being omitted from measurements. The length of the wing was measured from the center of the subalar area to the wing tip. No wing measurements were made of specimens with spread or curled wings. The ratio of eye width to genal width was determined with the head in perfect profile, the greatest possible measurement between anterior eye margin and posterior genal margin and between anterior eye margin and posterior eye margin being used.

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THE GENUS *NOMIA* IN THE NEW WORLD

The genus *Nomia* Latreille, 1805, (type species *Andrena curvipes* Fabricius) is a large (Dalla Torre, 1896, lists about 130 species), diverse group, widespread in distribution, with the bulk of its species in Africa, Asia and Australia. It is represented in the New World by approximately twenty species which may be divided among four subgenera: *Epinomia* Ashmead, *Acunomia* Cockerell, *Dieunomia* Cockerell, and *Paranomia* Michener.* These

* Michener, 1944, pointed out that *Paranomia* Friese is preoccupied (Conrad, 1860) and proposed *Paranomia* as a substitute, retaining *N. chalybeata* Smith as the type. *Curcinomia* Michener, 1944, named in the same paper (type *N. californiensis* Michener), is a synonym of *Paranomia* (new synonymy) and has line precedence over it. However, it is felt that *Paranomia* should take preference over *Curcinomia* because the former is based upon the original type of *Paranomia* (See Copenhagen Decisions on Zoological Nomenclature, 1953, page 67). Moreover, the status of *N. californiensis* is in doubt.

In placing certain American species in the same subgenus as *N. chalybeata*, I follow Cockerell, 1930.

subgenera comprise two diverse groups, those with bright integumental bands on the metasoma and those with bands of hair on the metasoma. The first group embraces *Paranomina* and *Acunomia*. The latter is restricted to the Americas while the former is found in Asia (and Australia?) as well. The second group contains *Epinomia* and *Dieunomia*. Again, the latter is found only in the New World while the former also has close relatives in Asia and Australia. It seems probable, therefore, that invasions of *Paranomina*- and of *Epinomia*-like bees reached this continent from Asia independently, probably before mid-Tertiary time, since they do not now occur north of about 50 degrees north latitude and hence must have reached the Western Hemisphere when the Bering Strait area was relatively warm. These two stocks are probably ancestral, respectively, to *Acunomia* and *Dieunomia*.

The four New World subgenera are distributed in a similar manner, and range from southern Washington through Minnesota and Virginia, southward to Florida, central Mexico and Baja California.¹ One subgenus (*Acunomia*) is established on the Bahamas (*N. wickhami*)², and on Cuba (*N. robinsoni*). No records of *Nomia* are known from Central or South America except *N. (Hoplonomia) expulsa* Cockerell (Cockerell, 1930) from French Guiana, and *N. (Dieunomia) heteropoda* (Say) from Brazil (see Michener in Musebeck, *et al.*, 1951, p. 1129). Both records are apparently incorrect. The distribution of these subgenera thus leaves little, if any, clue as to their origin and phylogeny. *Acunomia* is the most widespread, *Dieunomia* the least.

Acunomia and *Paranomina*, although easily separable, are morphologically similar. The relationship between *Epinomia* and *Dieunomia* is not as easily perceived. Certain *Dieunomia*, *e. g.* *N. heteropoda* (Say), differ greatly from the *Epinomia*, and certain authors have regarded *Dieunomia* as a distinct genus. Examination of the various species of *Dieunomia*, however, shows a continuous gradient of morphological divergence from the *Epinomia* group, commencing with *Nomia (Dieunomia) bolliana* Cockerell, whose female shows a striking resemblance to the female of *N. (Epinomia) triangulifera* Vachal.

Further evidence of the close relationship between *Dieunomia* and *Epinomia* has been found in the nest structure. Nests of *N. (Epinomia) triangulifera*, *N. (Epinomia) nevadensis*, and *N. (Die-*

1. Provancher's *N. compacta* (1889) from Quebec may be a small *Epinomia*, but because its description is ambiguous, and since its type locality is so far from the known range of any other *Epinomia*, it is not included in this paper, and is presumed to belong to some other genus.

2. I have not seen specimens of *N. wickhami* Ashmead, but infer from Cockerell's description (1910), that it, like *N. robinsoni*, belongs in *Acunomia*.

unomia) *heteropoda* are similar to one another and strikingly different from those of *N. (Acunomia) melanderi* Cockerell (Cross and Bohart, in press).

KEY TO THE AMERICAN SUBGENERA OF NOMIA

1. Metasomal terga without hair bands, with apical pale green, bluish, yellow, or coppery integumental bands 2
Metasomal terga with apical hair bands (often worn off), without integumental bands 5
2. (1) Males 3
Females 4
3. (2) Ultimate segment of antenna acuminate or at least acutely pointed, usually narrower than those preceding; basal vein of forewing only slightly arcuate; fifth metasomal sternum with median subapical processes contiguous or nearly so, arising from median longitudinal line *Acunomia*
Ultimate segment of antenna blunt, always as wide as or wider than penultimate segment; basal vein of forewing slightly to distinctly arcuate; fifth metasomal sternum with median subapical processes distinctly separated from the median longitudinal line (except in *N. fedorensis* which resembles *Acunomia* in this respect) *Paranomia*
4. (2) Middle tibial spur finely and almost evenly serrate along entire margin; basal vein of forewing slightly to distinctly arcuate, ... *Paranomia*
Middle tibial spur with but a few, uneven, coarse teeth along apical one third, basal two thirds finely and evenly serrate; basal vein of forewing only slightly arcuate *Acunomia*
5. (1) Males 6
Females 7
6. (5) Labial palpus with segments two to four together shorter than, rarely as long as, the first segment alone. Apical antennal segment distinctly wider than penultimate segment, flattened and expanded, sometimes disclike; tegula somewhat rectangular in shape, sinuate along lateral margin; length 10-23 mm., ... *Dieunomia*
Labial palpus with segments two to four together longer than first segment alone. Apical antennal segment not wider than penultimate segment, somewhat flattened but obliquely rounded distally, not expanded and disclike; tegula as described for *Dieunomia* or distinctly rounded posterolaterally; length 7-15 mm. *Epinomia*
7. (5) Labial palpus with segments two to four together rarely as long as first segment alone; pubescence of metasomal venter black, brown, deep orange, or reddish; tegula as in males; length 10-23 mm. *Dieunomia*
Labial palpus with segments two to four together longer than first segment alone; pubescence of metasomal venter white, greyish, buffy, or light golden yellow; tegula as for males; length 8-15 mm. *Epinomia*

Using the above key, the names of the American species, as listed by Michener, in Musebeck *et al* (1951), may be placed as follows:

Epinomia

- boharti* sp. nov.
- micheneri* sp. nov.
- nevadensis* Cresson
- triangulifera* Vachal

Paranomina

- californiensis* Michener
- fedorensis* Cockerell
- foxii* Dalla Torre
- maneei* Cockerell
- mesillensis* Cockerell
- parksii* Cockerell
- tetrazonata* Cockerell
- universitatis* Cockerell
- uvaldensis* Cockerell
- zabriskii* Cockerell and Blair

Dieunomia

- apacha* Cresson
- bolliana* Cockerell
- heteropoda* (Say)
- mesillae* (Cockerell)
- xerophila* (Cockerell)

Acunomia

- melanderi* Cockerell
- nortoni* Cresson
- robinsoni* Cresson
- wickhami* Ashmead

Subgenus EPINOMIA Ashmead

Epinomia Ashmead, 1899, Trans. Amer. Ent. Soc., vol. 26, p. 88. Type, (*N. persimilis* Cockerell) = *Nomia triangulifera* Vachal, monobasic and original designation.

Diagnosis: This subgenus may be separated from its closest relative, *Dieunomia*, by the lengths of the segments of the labial palpi as indicated in the key. The apical antennal segment of male *Dieunomia* is distinctly wider than the penultimate segment, while in male *Epinomia* the apical segment is the same width as the penultimate. Females of *Epinomia* may be separated from those of *Dieunomia* by the color of the hairs of the abdominal venter. In *Epinomia*, these are white, greyish, buffy, or golden yellow (somewhat rufous in Mexican specimens of *N. (Epinomia) nevadensis arizonensis*, while in *Dieunomia* they are black, brown, deep orange, or rufous. *N. bolliana* Cockerell, the smallest of the species of *Dieunomia*, is perhaps the only species of that subgenus that can be confused readily with species of *Epinomia*. In addition to the above-mentioned characters, *N. bolliana* may be known from *N. triangulifera* by the shape of the horizontal rugose base of the propodeum, which is distinctly crescentic, and by the lack of striations on the anterior lateral margins of the prothorax, from *N. boharti* by the lack of impunctate transverse ridges on the first two metasomal terga, and from other species of *Epinomia* by the shape of the tegulae, which are rectangular and sinuate along their lateral margins.

Description: Male: Length 7-15 mm.; color variable, ranging from wholly black to wholly fulvous or fulvo-ferruginous except for portions of the head and mesosoma; wings yellowish-hyaline to darkly fuliginous.

Pubescence of entire body pale greyish white to light ochraceous-buff, color usually uniform on any one specimen; face, posterior margin and lobes of pronotum, posterior margin of metanotum, axilla, and propodeal spiracles all densely clothed with downy, plumose hairs; metasomal terga one to five with distinct apical bands of appressed hair, that of sixth tergum indistinct.

Segments two to four together of labial palpus longer than the first alone; apical antennal segment somewhat flattened, obliquely rounded, or almost truncate, not expanded or wider than the preceding segment; face appearing round or elliptical, eyes subparallel or slightly convergent below, inner eye margins never strongly curved, not strongly convergent above; tegula rectangular, sinuate on lateral margin, or rounded posterolaterally, thus appearing oval; basal vein of forewing only slightly arcuate; hind basitarsus usually shorter than, not distinctly longer than hind tibia; hind tibia expanded distally except in *N. boharti* where the dilation is very slight; inner apical angle of hind tibia produced, forming a distinct tooth or nodule, a median tooth along inner edge present or absent; hind femur never greatly swollen, not wider than distance between lateral ocelli; hind trochanter with or without a ventral apical nodule; middle tibia and femur unmodified; dorsal base of propodeum with a horizontal, strongly rugose area which may be either crescent-shaped or distinctly truncate posteriorly; anterior face of the first metasomal tergum with a deep, longitudinal excavation; fourth metasomal sternum with a pair of distinct, arcuate sutures, meeting posteriorly to form a median triangular area, or sutures becoming mere impressions except posteriorly, or absent entirely; fifth metasomal sternum with a pair of pubescent subapical nodules and a pair of arcuate carinae converging posteriorly to form a median triangular area; apex of sixth metasomal sternum recurved and with a deep median cleft; seventh metasomal sternum ribbon-like; eighth metasomal sternum produced to a long acuminate process posteriorly; gonostyli converging evenly, not abruptly bent mesad, modified setae on ventral portions of apices in the form of a few thick bristles; gonostyli each with a posteriorly directed ventral process.

Female: Length 8-15 mm., form more robust than male; downy plumose pubescence as in male except that of face, which is greatly

reduced; hair bands distinct on metasomal terga one to four, fifth tergum bearing densely appressed pubescence of various shades from seal brown to bright rufous, sometimes also with an indistinct hair band anteriorly; color of pubescence white to rufous, often varied on any one specimen; pubescence of metasomal venter long, white to golden yellow, becoming rufous in some Mexican specimens of *N. nevadensis arizonensis*, face wider than in male; other structural characters as given in description of male.

Habits: Information concerning the habits of *Epinomia* is scanty, and much remains to be done in this respect. Bohart (1952, also in litt.), Cockerell (1934), Cross and Bohart (in press), Linsley and MacSwain (in litt.), Pierce (1904), Rau (1929), and Snelling (in litt.) have studied *N. triangulifera* and *N. nevadensis*.

These bees nest gregariously, often in large densely populated sites, but insofar as known they are true solitary bees, each female digging and provisioning one or more nests in a season, after which she dies, leaving her progeny to repeat the cycle the ensuing year. Adults generally appear in middle or late summer, although there is some evidence of a longer season in areas having summer rains where it is possible that several generations occur in the same year.

Insofar as known, the females prefer the flowers of various composites. G. Bohart (in litt.) mentions the possible importance of this group in areas where sunflower seed is grown for oil.

KEY TO THE AMERICAN SPECIES OF THE SUBGENUS EPINOMIA

1. Anterior lateral portion of prothorax with a series of vertical or nearly vertical striations; basal area of propodeum distinctly truncate posteriorly; tegula somewhat rectangular in shape, lateral margin distinctly sinuate; dark species, 11-15.5 mm. long *triangulifera*
- Anterior lateral margin of prothorax without striations; basal area of propodeum crescent-shaped or weakly truncate posteriorly; tegula as in *N. triangulifera* or rounded posterolaterally, appearing somewhat oval; species dark or with varying amounts of fulvous or ferruginous, 7-12.5 mm. long 2
2. (1) Males 3
- Females 5
3. (2) Hind tibia with distinct median excavation and usually with a tooth basal to it along anterior inner edge (fig. 4, G, H), ... *nevadensis*
- Hind tibia without median tooth or excavation along anterior inner edge 4
4. (3) Hind tibia greatly expanded distally, apex (including tooth) half as wide as length of segment; tegula rounded posterolaterally, appearing somewhat oval in shape; clypeal margin with a

- single, rectangulate median process*, the apex of which is not sinuate (fig. 3, F, G)..... *micheneri*
Hind tibia not greatly expanded distally, apex (including tooth) not half as wide as length of segment; tegula as described for *triangulifera*; clypeal margin with a single median process, the apex of which is distinctly sinuate (fig. 3, I)..... *boharti*
5. (2) First two metasomal terga each with a distinct, transverse, sub-apical, rounded carina that is impunctate and shining; tegula as described for *N. triangulifera*..... *boharti*
First two metasomal terga without carinae as described above; tegula rounded posterolaterally, appearing rather oval..... 6
6. (5) Apical margin of clypeus with a pair of distinct median teeth † (fig. 3, K)..... *micheneri*
Apical margin of clypeus not dentate..... *nevadensis*

Nomia (Epinomia) triangulifera Vachal

(Fig. 1; 3A, E, I; 4 A, E)

Nomia triangulifera Vachal, 1897, *Miscellanea Entomologica*, vol. 5, p. 9. (male).

Nomia persimilis Cockerell, 1898, *Denison Univ. Sci. Labs. Bull.*, vol. 11, pp. 50, 72; and *Bull. Univ. New Mexico*, vol. 1, pp. 50, 72.

Diagnosis: Although the females of this species superficially resemble *N. (Dieunomia) bolliana*, either sex may be readily separated from the latter, as well as from any species of *Epinomia*, by the presence of a series of vertical or nearly vertical striations on the lateral anterior portions of the prothorax. *N. triangulifera* is also separable from all other forms of *Epinomia* except *N. nevadensis bakeri* by the shape of the horizontal rugose base of the propodeum, which is truncate rather than crescent-shaped, and from all forms of *Epinomia* except *N. boharti* by the shape of the tegulae, which are rectangulate.

Description of male:

Size: Length 12-15.5 mm.; length of forewing 9.0-12.5 mm.; width of face 2.9-3.2 mm.; length of face 3.0-3.7 mm.

Color: Usually wholly black, two basal metasomal segments occasionally somewhat piceous; legs black to piceous; antenna black or becoming reddish beneath; tegula translucent-testaceous to dark brown; wings with a dull orange or brownish tint or subhyaline, apical one fifth infusate, sometimes lightly so; veins and stigma yellow-brown to dark brown.

Pubescence: Pale throughout, that of head, sides and venter of mesosoma and femora and tibiae of legs white or grayish white; that of mesonotum greyish or pale buffy white, densest on anterior

* Seen best from beneath.

† Seen from beneath.

one third; fasciae of metasomal terga one to five white; metasomal sterna two and three with several thin rows of long, shortly-plumose hairs and with short, subapical fringes of feathery plumose setae which are recurved medially, particularly on sternum three, and which are prolonged laterally to form tufts; sternum four with a thin apical fringe, also becoming tufted laterally; middle femur beneath with a few, scattered, short bristles; front femur beneath evenly and sparsely covered with tiny setae.

Punctuation: That of clypeus very fine, subcancellate, becoming coarser above, that of vertex coarser and sparser, areas about ocelli often minutely reticulate; punctures of mesoscutum close, coarse, similar to those of vertex, those of mesoscutellum coarser, variable in size and distribution, sparsest medially; first four metasomal terga with very fine and close punctures, the first, and sometimes the second with two distinct sizes, the coarser usually sparsely and evenly distributed among the finer; punctures of tergum five about as fine as the finer punctures of the first four but more sparse. All punctured surfaces moderately shining.

Structure: Apical margin of clypeus with a wide, slightly produced truncation (fig. 3, E); first flagellar segment almost as long as second, segments two to ten approximately equal in length, about .48 mm. each, apical (11th) segment longer, about .65 mm; face almost round, ratio of length to width 1:1.00-1:1.08; genal area about one and one quarter times as wide as eye; labial palpus with segments two to four together distinctly longer than first free segment alone; anterior lateral portion of prothorax with a series of vertical or nearly vertical striations; tegula with posterolateral angle rather abrupt, appearing somewhat rectangular, shallowly sinuate along lateral margin; horizontal rugose basal area of propodeum truncate posteriorly, somewhat polished; posterolateral angles of propodeum distinctly angulate, becoming sharply carinate ventrally; first three metasomal terga with shallow transverse basal constrictions; hind trochanter quadrate, without ventral nodule; hind femur as described for *N. nevadensis*; hind tibia expanded evenly distally, not excavated medially, roughly triangular in shape, anterior inner margin produced to form a large apical tooth (fig. 4, E); fourth metasomal sternum with a pair of distinct, arcuate sutures which converge posteriorly to form a median triangular area; tubercles of fifth sternum large, angulate, sinuate along posterior margin, reticulate, lacking conspicuous pubescence (fig. 4, A); apex of gonostylus as seen in ventral aspect acuminate-rounded (fig. 3,

A); length of ventral process of gonostylus about .54 mm.; ratio of length of ventral process of gonostylus to length of gonostylus about 1:2; subapical ventral margin of gonostylus with four to five distinct long rather stout bristles; laterodistal process of penis valve falcate.

Description of Female:

Size: Length 11.5-14 mm.; length of forewing 9.5-11.5 mm.; width of face 3.2-3.8 mm.; length of face 2.7-3.3 mm.

Color: As described for male except that antennae are sometimes wholly reddish.

Pubescence: That of face, sides and venter of mesosoma white, that of mesoscutum greyish-white to pale buffy-white; fasciae of metasomal terga one to four white, often worn on discs; fifth metasomal tergum with an apical fringe of thickly appressed, seal brown hairs, another row of appressed hairs just basad, these often lighter; apical one third of metasomal sterna two to six with very long hairs, thickest on sterna four and five, greyish white to buffy white tinged with gold; scopa long, white to buffy brown, hairs along posterior margin of hind tibia buffy white to brown admixed with buff; hairs on outer side of middle tibia whitish to buffy brown, admixed with bristles of seal brown.

Punctuation: Face punctured as in male; punctures of mesoscutum coarse and close, slightly larger than those of vertex, those of mesoscutellum variable in size but finer and much closer than those of mesoscutum; metasomal terga punctate throughout, the first two with fine and very close punctures, those of the third finer and somewhat sparser, those of the fourth still finer and distinctly more sparse than those of the third; under surfaces of front and middle femora as described for male; all punctured surfaces moderately shining.

Structure: Apical margin of clypeus with truncations as described for male, or truncation reduced or absent (fig. 3. J); face wider than that of male, ratio of length to width 1:10-1:19; genal area about one and one-fourth times as wide as eye; transverse basal constrictions of first three metasomal terga shallow, often nearly lacking, raised areas behind constrictions also lacking.

Variation: Despite its wide range, this species exhibits comparatively little interpopulational variation in the characters studied. Color variation is very slight, specimens from desert localities in New Mexico and Utah having at most the two basal terga fuscous rather than black. Size differences are apparent within populations

but are more difficult to establish between them. In one instance, the means of measurements of the facial width, calculated for males from two widely separated localities (Topaz, Utah and Lawrence, Kansas) and using sample sizes of 18 and 25 specimens, respectively, differed by only .125 mm. (3.479 mm.-3.354 mm.). A difference of means test applied to this difference, however, resulted in a significant "t" of 2.88, ($P < .01$) indicating that the means of the two populations were significantly different for the character tested.

No differences in wing color and punctation between populations were found, although intrapopulational variation was observed. A slight difference in the pubescence of the legs was found to exist between females from the Utah populations and those of the plains populations, a high percentage of the former exhibiting more brown hairs on the outer sides of the middle tibiae and along the posterior margins of the hind tibiae.

Distribution: Central and west central United States, from southern Kansas and New Mexico, north to central Minnesota and southern North Dakota, and from central Illinois west to western Utah (fig. 1).

Type material: The location of the type of *triangulifera* is not known to me. A lectotype female of *persimilis* from Las Cruces, New Mexico (Ckll. # 4885) is here designated and returned to the University of Nebraska collection.

Specimens examined: COLORADO: Alamosa, Elbert. ILLINOIS: Meredosia. IOWA: Sergeant's Bluff, Sioux City. KANSAS: De Soto, Douglas Co., Eudora, Hutchinson, Larned, Lawrence, Nickerson, Phillips Co., Syracuse. MINNESOTA: St. Paul. MISSOURI: Amazonia, Clay Co., St. Louis. NEBRASKA: Cedar Bluffs, Lincoln, Mitchell, Nebraska City, Omaha, West Point, Wymore. NEW MEXICO: Albuquerque, Las Cruces, Montoya. NORTH DAKOTA: Mcleod, Mott. SOUTH DAKOTA: Elk Point. UTAH: Lampo, Penrose, Promontory, Topaz.

Total number of specimens examined: 254 males, 148 females. The majority of these were caught between Aug. 10, and Sept. 15. Males have been found as early as July 7, and females as late as Oct. 2. No difference as to flight season between eastern and western populations is discernible.

Flower Records: *Bidens involucrata*, 1 ♂, 4 ♀; *Cleome serrulata*, 2 ♂; *Gilia* spp., 2 ♂; *Grindelia squarrosa*, 1 ♂, 1 ♀; *Grindelia*, spp., 2 ♂, 2 ♀; *Helianthus annuus*, 16 ♂, 36 ♀; *H. lenticularis*, 5 ♂, 7 ♀; *H. maximiliani*, 4 ♂; *H. petiolaris*, 1 ♂; *Helianthus* spp., 14 ♂, 4 ♀;

Medicago sativa, 1 ♀; *Polygonum* spp., 3 ♂; *Rudbeckia triloba*, 1 ♂, 1 ♀; *Silphium perfoliatum*, 4 ♂, 2 ♀; *Solidago* spp., 2 ♂; *Vernonia* spp., 3 ♂.

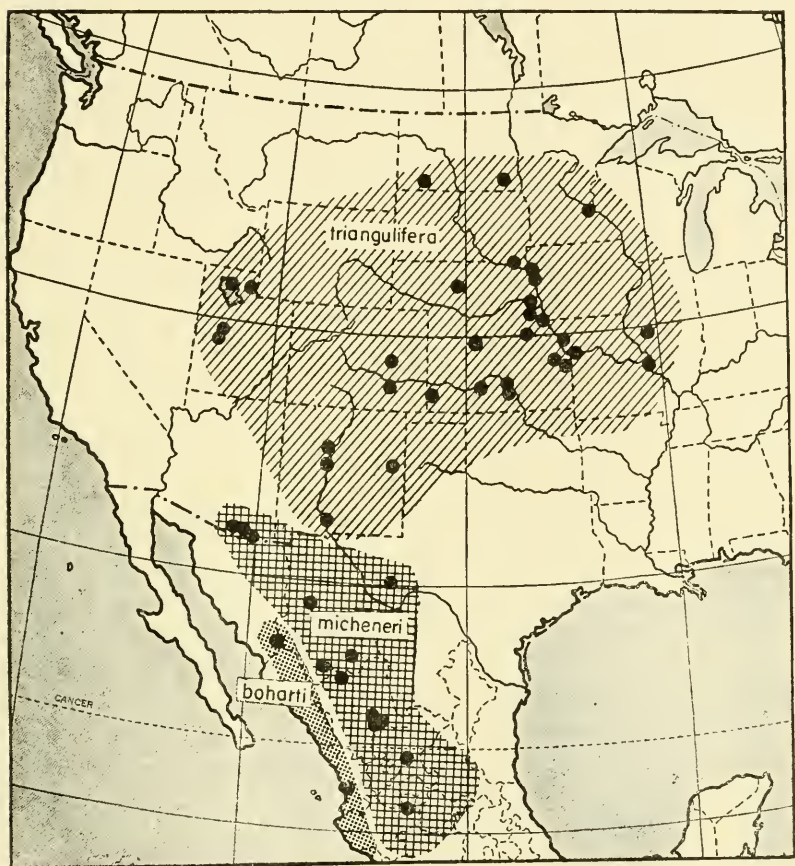


FIG. 1. Map showing the distribution of *N. (Epinomia) boharti*, *N. (E.) micheneri*, and *N. (E.) triangulifera*.

Nomia (Epinomia) micheneri,* sp. nov.

(Figs. 1; 3B, F, G, K; 4B, F)

Diagnosis: This rather large, variably colored species is sympatric with *N. nevadensis arizonensis* throughout much of its range and superficially resembles that form. The males are immediately separable from those of the other *Epinomia* by the margin of the clypeus, which bears a single rectangulate median process, the apex of which

* This species is named for Dr. Charles D. Michener, University of Kansas.

is not sinuate. The hind tibia of the male is also distinctive, being broadly dilated apically and lacking a median excavation on the anterior inner edge, somewhat resembling that of *N. triangulifera*. Unlike *triangulifera*, however, the large inner tooth is subapical rather than apical (fig. 4, F).

Both sexes may be distinguished from *triangulifera* by the absence of striations on the anterior lateral portions of the prothorax and by the shape of the horizontal rugose basal area of the propodeum, which is crescentic. They may also be distinguished from *triangulifera*, as well as from *boharti*, by the shape of the tegulae, which are rather arcuate posterolaterally.

In the northern parts of its range, *micheneri* is distinctly larger than *nevadensis arizonensis*, but in central Mexico the two species are commonly equal in size (see section on variation). Like *nevadensis*, the color of *micheneri* may range from wholly black to partly fulvo-ferruginous. In partially red males, however, the first metasomal tergum alone is usually fulvo-ferruginous, while such males of *nevadensis* usually have the first two metasomal terga colored. The females are rather difficult to distinguish from those of *nevadensis*, the most distinct character being a pair of small teeth situated medially on the apical margin of the clypeus. Also, partially red females of *micheneri* usually have only the first two metasomal terga fulvo-ferruginous, while those of *nevadensis* generally have the first three terga of that color. The mesoscutellum of *micheneri* often bears a pair of mediolateral impunctate areas which are usually lacking in *nevadensis*.

Description of male:

Size: Length: 12.1 mm. (9.0-12.1); length of forewing 11.4 mm. (9.2-11.8); width of face 2.89 mm. (2.38-2.92).

Color: Head black; mesasoma black (or posterior portion of mesonotum fulvo-ferruginous); metasomal terga two to five black, metasomal tergum one and the apex of tergum two fulvo-ferruginous (metasomal terga wholly black to first two and part of third fulvo-ferruginous); coxae fuscous (to black); trochanters fuscous (to black); fore and middle femora piceous basally, becoming fusco-fulvous distally (or entirely black); posterior femora fulvo-ferruginous (to black); antennae darkly fuscous (wholly black to fuscous with reddish beneath); tegulae translucent testaceous (to dark testaceous); wings yellowish hyaline (to brownish hyaline), apical one fifth infuscate, nervures and stigma yellow-brown to dark brown.

Pubescence: Pale throughout, similar to that described for the

male of *N. boharti*. Head, sides and venter of thorax, and femora and tibiae with long greyish-white hairs, those of mesoscutum thin, buffy white (or greyish white); fasciae of metasomal terga one to five white (to buffy white); metasomal terga one to five with several thin rows of long, rather stout, posteriorly directed hairs just basad of fasciae (not as prominent on tergum one in some), rest of these terga sparsely and evenly covered with shorter whitish hairs (or these as long as prefascial hairs); subapical fringes of short hair on metasomal sterna two and three as described for *N. boharti* (more distinct in some *micheneri*), apical fringe of sternum four absent (rather dense, long subapical fringe sometimes present); middle femora beneath bare and shining medially, front femora also bare beneath medially, patches of tiny setae present posterobasally, apically, and along anterior margin.

Punctuation: That of clypeus and paracocular areas close and coarse, that of vertex coarser and sparser except behind ocelli, deeper than that of *boharti*; punctures of mesoscutum only a little coarser than those of vertex, about as close, those of mesoscutellum variable in size (to almost uniform in size), densest around periphery and along median scutellar line, sparser mediolaterally (or having impunctate areas mediolaterally), with a medium polish; posterior surfaces of propodeum as described for *boharti*; punctuation of first tergum coarse and rather sparse basally, becoming finer and closer apically (to evenly and more finely punctate throughout), second tergum with punctuation as in apical portion of first, that of third finer and closer than that of second, that of fourth finer and as close as that of third, that of fifth still finer and closer than that of fourth; middle femora impunctate and polished beneath, except for a few variable punctures basally; front femora impunctate beneath medially, but having tiny, shallow punctures basally and anteroapically; all punctured surfaces with a medium polish.

Structure: Apical margin of clypeus with a single, narrow, rectangular process which differs from that described for *boharti* in that its apex is truncate rather than emarginate (fig. 3 F, G); antennae with first flagellar segment about five-sixths as long as second, segments two to ten equal in length, about .45 mm. (about .41 mm. in some specimens), apical longer, about .54 mm.; face wider than long, appearing rather elliptical, ratio of length to width about 1:1.14; labial palpi as described for *boharti*; eyes about as wide as genal areas behind them. Anterior lateral portion of prothorax smooth and shining except for a few scattered punctures;

tegula with posterolateral angle rather rounded, never abrupt; horizontal rugose basal area of propodeum crescent-shaped; posterodorsal angles of propodeum rounded, broadly so dorsally. Transverse basal constrictions of first three metasomal terga as described for *boharti* but excavations more shallow. Hind trochanter quadrate, without ventral nodule; hind femur feebly carinate basally along both anteroventral and posteroventral angles, carina distinctly more pronounced along latter (in most, anteroventral carina subequal to posteroventral one); hind tibia expanded broadly apically, without median excavation, width at apex, including inner tooth, much more than half of length; inner tooth large, appearing subapical (fig. 4, F); fourth metasomal sternum without converging sutures (or a pair of sutures or impressed lines present, these converging posteriorly to form a median triangular area as described for *N. triangulifera*); tubercles of fifth sternum small, nodulate, not pubescent (fig. 4, B); apex of gonostylus as seen in ventral aspect acuminate (fig. 3, B); ventral process of gonostylus about .35 mm. long; ratio of length of ventral process to length of gonostylus 1:2.2; subapical ventral margin of gonostylus with two to five small indistinct bristles; laterodistal process of penis valve tuberculate.

Description of female:

Size: Length, 11.9 mm. (11.0-12.2); length of forewing 10.8 mm. (9.9-10.8); width of face 3.43 mm. (2.61-3.43); length of face 2.82 mm. (2.82-2.88).

Color: Head and mesosoma black (ferruginous spots on posterior face of propodeum in one specimen); antennal scape fusco-fulvous (to fuscous), flagellum black; metasomal terga three to five black, except for a narrow fusco-fulvous line basad of the fasciae on terga three and four (or fusco-fulvous line restricted to tergum three or absent altogether); metasomal terga one and two fulvo-ferruginous; coxae and trochanters darkly fulvous to fuscous (or black), remaining leg segments fulvous except for basal one fourth of femora, which are fusco-fulvous (or remaining segments entirely fulvous); wing color as described for male but slightly darker.

Pubescence: Pale throughout, that of face, sides, and venter of mesosoma buffy white, that of mesoscutum sparse, pale ochraceous-buff; fasciae of metasomal terga one to four buffy white (to light ochraceous-buff); several thin rows of long stiff posteriorly directed hairs present just basad of fasciae on terga one to four (these absent or indistinct in some Mexican specimens) pale yellow to golden in color; apical fringe of tergum five rufescent; apical one third of

metasomal sterna two to five with long, light ochraceous-buff hairs; discs of terga one to five without feathery-plumose appressed hairs, but with sparse erect or suberect hairs; scopal hairs long, buffy white, hairs along posterior margin of hind tibia buffy white (or tinged with rufous); hairs on outer side of middle tibia buffy white tinged with rufous.

Punctuation: That of clypeus very coarse and close, that of vertex a little finer and sparser except behind ocelli; punctures of mesoscutum like those of vertex but very close, those of mesoscutellum like those of mesoscutum, densest around periphery and along median mesoscutellar line, leaving a pair of shining, impunctate lateromedian areas (not well defined in all specimens); metasomal terga punctate throughout, first two with medium-fine and rather close punctures, punctures of third finer and as close as those of second, those of fourth tergum still finer and somewhat closer than those of third; middle femur beneath with coarse sparse punctures basally and posteriorly, impunctate medially (or with a few scattered punctures); front femur beneath generously and evenly spotted with minute punctures, heaviest on basal two thirds.

Structure: Face about as wide as that of male but shorter (ratio of length to width 1:1.22 [1:1.18-1:1.25]); apical margin of clypeus with a pair of small median teeth similar to those described for *boharti* but less prominent; genal area about one and one-fourth times as wide as eye; first three metasomal terga only shallowly constricted basally, area immediately posterior to constriction not prominently raised.

Variation: *N. micheneri* is a polychromatic species comparable in color variation to certain forms of *N. nevadensis*. This variation has been stated as fully as possible in the description of the species, and no further discussion will be made here. Its geographical occurrence in males is shown in a general way in Table I. Because of the paucity of specimens and lack of reliable climatological data, no attempt will be made here to correlate climatic factors with color differences as was done with *N. nevadensis*, but it seems likely that a correlation exists as in that species.

Another important variable in *micheneri* is size. Table I will suffice to show that in males this character varies rather consistently in a general north-south direction with the largest specimens being from the northernmost portions of the range, a notable exception being the specimens from Jalostotitlán, Jalisco. Because of their distinct differences in size, it is felt that the specimens examined possibly represent more than one subspecies and it is for this reason

that only the northernmost specimens have been designated as types.

The specimens from Jalisco are indicative of the extreme variability which may be found in the species. Although reference to Table I indicates that only one male specimen from San Juan de Los Lagos was measured, two others were examined. Both were noticeably smaller than specimens from any other part of the species range, and in addition were partly red. Six miles northeast of Jalostotitlán, at a distance of only six miles from the above locality, a sample of ten very large, wholly black males was taken. Only males from southern Arizona and northern Chihuahua were larger than these.

The sutures of the fourth sternum of the male are highly variable. In both *micheneri* and *boharti*, these sutures may be absent, feeble and incomplete, or distinct and complete. They are invariably present in *nevadensis* and *triangulifera*.

Distribution: The species is apparently restricted to the Mexican Plateau and southern Arizona. Most of the specimens before me are from the mesquite-grassland or live-oak regions in higher altitudes, ranging up to 7500 feet.

TABLE I—Facial measurements (in mm.) and color variation in males ¹ of *Nomia* (*Epinomia*) *micheneri*

Localities	No. specimens	Color ² (in percent)		Mean, width of face ± S. E.	Mean, length of face ± S. E.
		Partly red	Wholly black		
So. Arizona ³	5	100	000	3.340 ±.032	2.860 ±.035
Matachic, Chihuahua	2	000	100	3.351	2.812
So. Chi- huahua ⁴	14	85	15	3.079 ±.028	2.585 ±.025
So. Durango ⁵	4	50	50	3.067 ±.067	2.515 ±.054
San Juan de los Lagos, Jalisco	1	100	000	2.862	2.416
Jalosto- titlán, Jalisco	10	000	100	3.174 ±.026	2.591 ±.028
León, Guanajuato	1	000	100	3.162	2.550

1. Females are not included because adequate samples of them were not available over most of the species range.

2. Because of the small number of specimens examined, a detailed listing of all color differences is impractical here. Specimens listed in the column headed "partly red" had at least the basal metasomal tergum fulvo-ferruginous.

3. Includes males from Sonoita (2); 10 miles east of Sonoita (1); 10 miles west of Bisbee (1); mouth of Carr Canyon. Huachuca Mts. (1).

4. Includes males from Santa Bárbara, Chihuahua (7); Ojito, Chihuahua (1); Jiménez, Chihuahua (4); Canutillo, Durango (2).

5. Includes males from San Lucas (2); San Juan del Río (1); Yerbanis (1).

Type material: Holotype male from Sonoita, Arizona, Aug. 9, 1940 (P. H. Timberlake); allotype female from 25 miles east of Sonoita, Aug. 9, 1924 (E. P. Van Duzee). Eight male and female paratypes as follows: one male from Sonoita, Aug. 9, 1940 (P. H. Timberlake), two males from ten miles east of Sonoita, Aug. 9, 1940 (E. S. Ross), one male from ten miles west of Bisbee, Arizona, Aug. 10, 1940 (E. S. Ross), one male from Carr Canyon, Huachuca Mts., Arizona, Aug. 10, 1940 (C. D. Michener), one male from near Ramsay Canyon, Huachuca Mts., Arizona (P. H. Timberlake), one female from Douglas, Arizona, Aug. 27, 1939 (R. H. Crandall), and one female from Alpine, Texas, July 7, 1942 (E. C. Van Dyke).

Type repositories: Holotype, allotype, one female and two male paratypes to the California Academy of Science, two male paratypes to the collection of Prof. P. H. Timberlake, one male paratype to the collection of Dr. G. E. Bohart, one male paratype to the Snow Entomological Museum at the University of Kansas, and one female paratype to the University of Arizona at Tucson.

Specimens examined: CHIHUAHUA: Matachic, July 7, 1947 (Rockefeller Exped.—Michener), 2 ♂; Santa Bárbara, July 17-18, 1949 (Rockefeller Exped.—Michener), 3 ♂, 1 ♀; July 17, 1947 (Rockefeller Exped.—Cazier), 3 ♂; Aug. 17, 1947 (G. M. Bradt), 1 ♂; Ojito, 36 kilo, St. Bárbara, Sept. 29, 1947 (G. M. Bradt), 1 ♂; 10 miles W. Jiménez, Sept. 11, 1950 (R. F. Smith), 4 ♂. DURANGO: 8 miles S. Canutillo, Aug. 9, 1951 (P. D. Hurd), 2 ♂; San Juan del Rio, Aug. 7, 1951 (H. E. Evans), 1 ♂; San Lucas, Aug. 2, 1947 (Rockefeller Exped.—Michener), 2 ♂; Yerbánis, Aug. 19, 1947 (Rockefeller Exped.—Michener), 1 ♂. ZACATECAS: Fresnillo, Aug. 15, 1947 (Rockefeller Exped.—Michener), 1 ♂. JALISCO: San Juan de los Lagos, July 27, 1951 (P. D. Hurd), 3 ♂; Jalostotitlán, July 19, 1954 (Univ. Kans. Mex. Exped.) 10 ♂. GUANAJUATO: 6 miles N.W. León, Aug. 9, 1954 (Univ. Kans. Mex. Exped.), 1 ♂.

Flower records: No flower records are available for the females, but three males have flower labels attached as follows: Yerbánis, Durango, on *Helianthus*; Canutillo, Durango, on *Guardiola tulo-carpa*; and San Juan de los Lagos, Jalisco, on *Eysenhardtia polystachya*.

Nomia (Epinomia) boharti,* sp. nov.

(Figs. 1; 3D, I, N; 4D, I)

Diagnosis: This rather small black species most nearly resembles certain black subspecies of *N. nevadensis*. It is immediately sepa-

* This species is named in honor of Dr. George E. Bohart, U. S. Legume Seed Research Lab., Logan, Utah, without whose guidance and encouragement this paper would not have been written, and from whose private collection the type series was taken.

rable from the latter group, however, by the shape of the tegula, which has the posterolateral corner abruptly bent in the same manner as *N. triangulifera*. The males may be distinguished from those of any other *Epinomia* by the distinctive shape of the hind tibia and the shorter antenna. The females are likewise separable from others of the subgenus by the presence of highly polished, impunctate ridges immediately basad of the fasciae on metasomal terga one to three (more distinct on terga one and two).

Description of Male:

Size: Length 10 mm. (9.7-10.4); length of forewing 9.5 mm.; width of face 2.9 mm. (2.82-3.02); length of face 2.55 mm. (2.51-2.58).

Color: Head, mesosoma, and metasoma black; legs black to piceous; antenna black, becoming fuscous beneath (or entirely black); tegula very pale testaceous, subhyaline; wings brownish hyaline (hyaline to yellow-brown hyaline), veins and stigma yellow brown to dark brown.

Pubescence: Generally pale and rather sparse, hairs often shortly plumose; hairs of head, sides and venter of mesosoma, and femora and tibiae white to greyish white (or buffy white), pubescence of mesoscutum sparse, greyish white (to buffy white); fasciae of metasomal terga one to five buffy white to ochraceous-buff; terga three to five with several thin rows of long, rather pale, yellowish hairs just basad of fasciae, tergal discs otherwise evenly covered with whitish (to pale ochraceous-buff) suberect hairs, these becoming much longer laterally; subapical fringes of short hair on the second and third metasomal sternum barely evident, not recurved; apical fringe of fourth sternum absent, subapical fringe present; middle femur beneath clear and shining but for a patch of small setae posterobasally; front femur bare and shining except for a patch of fine basal setae and a few coarse, scattered hairs anteriorly.

Punctuation: That of clypeus and paraocular areas close and coarse, that of vertex much sparser and coarser; mesoscutum shining, punctures as sparse as those of vertex but coarser and deeper, those of mesoscutellum similar to those of posterior one third of mesoscutum, densest around periphery and along median scutellar line, sparser in mediolateral areas; dorsolateral angles of propodeum almost impunctate, brightly shining, posterior face of propodeum also shining, very coarsely and sparsely punctate; punctuation of first and second metasomal terga moderately fine, even and close, third more finely punctate than the first two, fourth with punctures finer but no closer than those of third; middle femur beneath impunctate ex-

cept for a few fine punctures basally and posteriorly, front femur beneath with only a few tiny basal punctures and larger scattered punctures along anterior margin; integument in general highly polished.

Structure: Apical margin of clypeus with a rather narrow, emarginate protuberance (fig. 3, I); antenna noticeably shorter than in other male *Epinomia*, first flagellar segment about three-fourths as long as second, segments two to ten equal in length, about .34 mm. each, apical (11th) segment longer, about .39 mm.; face wider than long, appearing elliptical, ratio of length to width 1:1.15 (1:1.13-1:1.17); labial palpus with segments two to four together shorter than those described for *N. triangulifera*, but still distinctly longer than the first segment alone; eye a little wider than genal area behind it; anterior lateral portion of prothorax smooth, shining, nearly impunctate; tegula with posterolateral angle rather abrupt as described for *N. triangulifera*, lateral margin shallowly sinuate; horizontal rugose basal area of propodeum crescent shaped; dorsolateral angles of propodeum rounded, broadly so dorsally; transverse basal excavations of terga one to three deep (that of tergum three shallower than basal two), the areas immediately posterior raised, first three terga thus appearing corrugated when viewed in profile; hind trochanter quadrate, without ventral nodule; hind femur with posteroventral angle sharp (to carinate), anteroventral angle rounded; hind tibia expanded only slightly apically, width at apex, including inner tooth, much less than half the length (fig. 4, I); inner tooth small, barely subapical; anterior inner margin of hind tibia without a median excavation; fourth metasomal sternum without converging sutures (or a pair of sutures or impressed lines present, these converging posteriorly to form a median triangular area as described for *N. triangulifera*); tubercles of fifth sternum wide, rounded on posterior margin, with conspicuous bladelike setae (fig. 4, D); apex of gonostylus as seen in ventral aspect, emarginate, with a dorsal, medially directed, pubescent, triangular flange, (fig. 3, D); length of ventral process of gonostylus about .4 mm.; ratio of length of ventral process of gonostylus to length of gonostylus about one to two; subapical ventral margin of gonostylus with about eight short, spinose setae; laterodistal process of penis valve tuberculate.

Description of female:

Size: Length 9.5 mm.; length of forewing 9.4 mm.; width of face 2.9 mm.; length of face 2.4 mm.

Color: That of head and mesosoma as in male, metasoma fuscous (to black); legs fuscous, antennae tinged with reddish (to black); tegulae as in male; wings yellow-brown (to brownish-hyaline), apical one fifth lightly infusate (to darkly infusate); veins and stigma yellow-brown to dark brown.

Pubescence: That of face, sides and venter of mesosoma buffy white (to grayish white); dense, downy plumose pubescence of dorsolateral angles and lobes of pronotum, mesonotum and axillae light ochraceous-buff (darker on Nayarit female); hairs of mesoscutum sparse, light ochraceous-buff (to ochraceous-buff); fasciae of metasomal terga one to four light ochraceous-buff, apical fringe of fifth tergum buffy, with a tinge of rufous; stiff, posteriorly directed prefascial hairs absent; discs of terga one to five without feathery-plumose appressed hairs; apical halves of metasomal sterna two to five densely covered with long, light buff hairs; scopa buffy, hairs along posterior margin of hind tibia ochraceous to pale rufous; hairs on outer side of middle tibia buffy, becoming ochraceous to pale rufous apically.

Punctuation: That of clypeus coarse and close, that of vertex a little coarser and much sparser; punctures of mesocutum about as coarse as those of vertex but closer, those of mesoscutellum like those of mesoscutum, densest around periphery and along median mesoscutellar line, leaving a pair of shining, impunctate latero-median areas; metasomal terga one to three each with a distinctly shining, impunctate, transverse ridge just basad of fascia, more prominent on terga one and two, terga otherwise punctate throughout; punctures of first metasomal tergum as described for male, that of second closer and finer than that of first, that of third much finer (one half the size of those on terga one and two) and slightly closer than that of second; middle femur beneath with a few coarse punctures basally and posteriorly, front femur beneath generously spotted with minute shallow punctures.

Structure: Face no wider than that of male, facial length-to-width ratio also as described for male; apical margin of clypeus with a pair of median teeth separated by about twice the width of one of their bases, margin between them sinuate (fig. 3, N); width of genal area subequal to that of eye; first three metasomal terga strongly excavated basally, the first two more so than the third, areas immediately posterior to excavations distinctly raised, impunctate, and with a high polish.

Variation: Both sexes from Nayarit exhibit darker pubescence

and antennae than those from San Bernardo. Because of the small sample sizes at hand, it was therefore deemed best to exclude the former population from the type series. Intrapopulational variation includes size, shape and size of the protuberances of the clypeal margin, and, in the male, the presence or absence of the posteriorly converging sutures of the fourth sternum. These last two characters are also variable in *N. micheneri* but remain constant in *N. triangulifera* and *N. nevadensis*.

Distribution: Apparently restricted to the forested areas of western Mexico.

Type material: Holotype male, allotype female, and three paratypes, San Bernardo, Sonora, Mexico, Aug. 16, 1935 (collector unknown).

Type repositories: Holotype and allotype to the California Academy of Sciences, one paratype to the University of California at Davis, one paratype to the private collection of Dr. G. E. Bohart, and one paratype to the Snow Entomological Museum at the University of Kansas.

Specimens examined: NAYARIT: 5 mi. E. San Blas, Elev. 25 ft., July 25, 1953 (Kans. Univ. Exped.), 5 ♂, 1 ♀.

Habits: Nothing is known of the habits of this species. The Nayarit series was taken on an unidentified yellow composite which grew in open areas in a tropical forest. Several of the males from the same series had mud caked on the hind tibiae and presumably had recently been underground.

Nomia nevadensis Cresson

This widespread polychromatic species occurs throughout the southern half of the United States and is found as far south as the state of Jalisco, Mexico. Five easily separable forms are found within this range, and these have been retained (or designated) as subspecies to show their close relationship. In a paper yet to be published, the author has attempted to associate various climatic factors with the integumental color of this species. There is evidence that such color is well correlated with relative humidity.

The following characters will facilitate separation of this species from the remaining *Epinomia*.

Diagnosis: Both sexes may be separated from specimens of *N. triangulifera* by the absence of striations on the anterior lateral portion of the prothorax. The males are separable from those of the other *Epinomia* by the shape of the hind tibia, which is broadly dilated apically, and which possesses a curved median excavation

(fig. 4, G, H). Females are distinguished from those of *boharti* by the shape of the tegula, which is rather arcuate posterolaterally, and by the absence of impunctate, shining ridges on the first three metasomal terga. They are more difficult to distinguish from those of *micheneri*, the most distinct characters being size (in the U. S. specimens) and the absence of distinct teeth on the apical margin of the clypeus. Both characters are somewhat variable; the distinctive characters are further discussed under *N. micheneri* and reference to the descriptions and to the diagnosis of the latter species is advised.



FIG. 2. Map showing the distribution of *N. (E.) nevadensis*.

Nomia nevadensis nevadensis Cresson

(Figs. 2; 3C, H; 4C, H)

Nomia nevadensis Cresson, 1874, Trans. Amer. Ent. Soc., vol. 5, p. 101; also Cresson, 1875, in Wheeler, Report upon Geographical and Geological Explorations and Surveys West of the 100th Meridian . . . Vol. 5 (Zoology), p. 722, Pl. XXXIV.

*Description of male: **

Size: Length 10.7 mm. (measured from a specimen from Fairbank Springs, Nev.); length of forewing 9.8 mm.; width of face 2.92 mm. (2.92-3.12); length of face 2.65 mm. (2.65-2.95).

Color: Face black but for apical margin of clypeus, which is fulvous (face entirely black to face black, clypeus admixture of fuscous and fulvous areas); mesosoma fuscous anteriorly, posterior one third becoming fulvous (to mesosoma entirely fulvous but for black mesoscutum); metasomal terga one to three fulvous, four and five fuscous (to metasomal terga one to two fulvous, three to five black); coxae and trochanters fuscous to fulvous, remaining segments of legs fulvous; antennae piceous above, becoming lighter beneath; tegulae translucent-testaceous (to hyaline), wings pale yellowish hyaline, nervures and stigma yellow brown to dark brown.

Pubescence: (The following is based upon specimens taken at Fairbanks Springs, Nevada, since the original types have been immersed in alcohol and the hair color has doubtless been altered.)

Pubescence pale throughout. Head, sides and venter of mesosoma, and femora and tibiae with greyish white hairs, that of mesoscutum moderately dense, thickest anteriorly, greyish white; fasciae of metasomal terga one to five buffy white; metasomal terga two to five with several thin rows of long, rather stout, posteriorly directed hairs just basad of fasciae, all terga otherwise covered evenly with shorter thin whitish hairs; subapical fringes of short hair on metasomal sterna two to three distinct, recurved, most prominent on sternum two; both apical and subapical fringes of sternum four present, dense, the subapical densest medially and laterally; middle femur bare and shining beneath medially (or with a few short bristles posteromedially); front femur beneath rather evenly and sparsely covered with microscopic setae, heaviest basally and along anterior margin.

Punctuation: That of clypeus moderately close and coarse, that of vertex coarser and sparser except behind ocelli; punctures of mesoscutum coarser than those of vertex (sometimes only slightly so), and about as close (or mesoscutal punctures closer than those of vertex); punctures of mesoscutellum of uniform size and distribution, slightly smaller than those of mesoscutum; posterior surface of propodeum as described for *boharti*; punctuation of first two metasomal terga moderately close and coarse (punctures of basal half of first sparser), punctures of third and fourth almost alike, slightly finer

* Except as otherwise noted, this description is based upon a specimen (lectallotype, designated below) of the original type series kindly lent to me by Dr. Harold Grant of the Academy of Natural Sciences of Philadelphia. Statements of variation in parentheses are based upon other material of the subspecies.

and closer than those of second, terga otherwise punctate throughout; middle femur impunctate and polished beneath except for a few punctures basally; all punctured surfaces with a medium polish.

Structure: Apical margin of clypeus with a wide, shallow, weakly emarginate process about seven times as wide as high, resembling that of *triangulifera* but more prominent (fig. 3, H); antenna with first flagellar segment about $\frac{1}{11}$ as long as the second, segments two to ten equal in length, about .39 mm. each, apical (11th) segment longer, about .58 mm.; face only slightly wider than long, appearing almost round, ratio of length to width 1:1.10 (1:1.05-1:1.10); eye about as wide as genal area behind it; labial palpus as described for *N. boharti*; anterior lateral portion of prothorax smooth and shining except for a few scattered punctures; tegula with posterolateral angle rather evenly rounded, not abruptly bent; horizontal rugose basal area of propodeum crescent shaped; posterodorsal angle of propodeum moderately rounded, not as angulate as those described for *boharti*; transverse basal constrictions of first three metasomal terga as described for *N. boharti*, but more shallow; hind trochanter quadrate, possessing a single conspicuous nodule on its inner apex; hind femur keeled but not distinctly carinate basally along anteroventral and posteroventral angles (or keeled along anteroventral angle and feebly carinate along posteroventral angle); hind tibia broadly expanded apically, width at apex, including distal inner tooth, much more than half the length of the segment, distal tooth only slightly subapical; anterior inner margin of hind tibia with a broad, curved, median excavation whose proximal margin becomes sharply angulate, hind tibia thus appearing to be two-toothed (fig. 4, G, H); fourth metasomal sternum always with a pair of distinct sutures which converge apically to form a median triangular area; tubercles of fifth sternum of moderate size, nodulate, reticulated, pubescent (fig. 4, C); apex of gonostylus as seen in ventral aspect tapering and rounded (fig. 3, C); ventral process of gonostylus long, about .65 mm.; ratio of length of ventral process of gonostylus to length of gonostylus 1:1.6; subapical ventral margin of gonostylus with two to four rather indistinct bristles; laterodistal process of penis valve falcate.

*Description of female: **

Size: Length 11.3 mm. (measured from a specimen from Fairbanks Springs, Nevada); length of forewing 9.7 mm. (9.7-9.9); width of face 3.1 mm. (3.1-3.2); length of face 2.7 mm. (2.7-2.9).

* This description, like that of the male, is based upon a specimen of the original type series.

Color: Head fuscous, lightest along clypeal margin (or head black, clypeus and supraclypeals largely fulvous); antennal scape fulvous, clavola fuscous, becoming lighter beneath; mesosoma fulvous, becoming somewhat fuscous anteriorly (mesosoma entirely fulvous to metasoma fulvous but for black mesoscutum); metasoma entirely fulvous; legs entirely fulvous; tegula translucent-testaceous; wings pale brownish-hyaline, nervures and stigma yellow-brown to dark brown.

Pubescence: (Described from Fairbanks Springs specimens as in male.) Pale throughout; hairs of face, sides and venter of mesosoma buffy white, those of mesoscutum ochraceous-white, short and rather dense; fasciae of metasomal terga one to four buffy white to ochraceous-white, apical fringe of tergum five rufescent; stiff, posteriorly directed hairs just basad of fasciae on terga one to four colored as fasciae or with a pale yellow tinge, discs of metasomal terga one to five covered with short, feathery-plumose, appressed hairs interspersed with suberect short hairs, the former most prominent on terga three and four, present only apically on the first tergum; apical one third of metasomal sterna two to five with long, ochraceous-white hairs, those of sterna four and five with a golden or rufous tinge at their bases; scopa buffy white, hairs along posterior margin of hind tibia buffy white; hairs on outer side of middle tibia buffy white or with a tinge of gold.

Punctuation: That of clypeus very coarse and rather sparse, that of vertex finer and closer, especially behind ocelli; punctures of mesoscutum like those of vertex but closer, those of mesoscutellum like those of mesoscutum, almost evenly distributed; metasomal terga punctate throughout, first with moderately fine and rather close punctures, those of second as close but distinctly finer, those of third still finer and a little closer than those of second, those of fourth yet finer and about as close as those of third; middle femur beneath with sparse, coarse punctures basally and posteriorly, bare and shining medially and apically; front femur beneath coarsely and evenly covered with minute punctures.

Structure: Face a little wider than that of male and shorter, ratio of length to width 1:1.125 (1:1.117-1:1.132); clypeus long, hiding mandibles when the latter are fully retracted; apical margin of clypeus with a wide, very shallow, median process, the margin of which is sinuate (superficially appearing bidentate in some), of this

process indistinct or absent; genal area slightly wider than eye; first three metasomal terga only shallowly constricted, areas immediately posterior to constrictions not prominently raised.

Variation: The specimens from eastern Nevada are slightly smaller than the Fairbanks Springs group and, in general, somewhat more darkly colored. In these respects, they resemble the nearby Utah populations, and it is probable that the area of the Nevada-Utah line is a zone of intergradation between *N. nevadensis nevadensis* and *N. nevadensis arizonensis*. The group from Fairbanks Springs appears to be isolated by Death Valley and mountains from populations to the west and south.

Distribution: Known only from Fairbanks Springs, Nye Co., Nevada, and from White Pine Co., Nevada.

Type locality: Cresson, in the description of the species, gives the following information regarding type locality: "8 male, female specimens, Eastern Nevada, 1872. H. C. Yarrow."

Dr. Yarrow, in his account (Wheeler, 1875) of the 1872 expedition on which the above specimens were collected, writes: "Lieutenant Hoxie's route was from Fairfield, Utah, making a detour westward to Fillmore, Utah . . ., and following quite closely the outward course of Captain Simpson in 1858 and 1859, the southern limit of the so-called American Desert was crossed, the extreme western limit reached being Schell Creek Valley, Nevada. From this point, the direction was south by east to Snake Creek Valley, due east across Confusion Range, . . . south to the crossing of the Sevier, a short distance above Deseret City, and thence to Fillmore." The above narrative leaves no doubt that the type specimens were collected in either White Pine County, Nevada, or in the extreme western portion of Millard County, Utah. It seems most likely that the former is correct, and that the specimens actually came from the vicinity of what is now McGill, Nevada.

Type repositories: Lectotype female, designated by Cresson (1916), and lectallotype male, here designated, as well as one male paratype are in the Academy of Natural Sciences of Philadelphia.

Specimens examined: NEVADA: Nye County; Fairbanks Springs, June 21, 1949 (C. B. & R. N. Phillip), 1 ♂, 1 ♀; same locality, June 23, 1951 (I. LaRivers, T. Frantz), 1 ♂, 3 ♀.

Nomia (Epinomia) nevadensis arizonensis Cockerell

(Figs. 2; 3L)

Nomia arizonensis Cockerell, 1899, Entomologist, vol. 32, p. 128.*Nomia nevadensis arizonensis* Cockerell, 1925, Pan-Pac. Ent., vol. 1, p. 179.

Description: As described for *N. nevadensis nevadensis* except as follows:

Smaller, width of face of male 2.41-3.10 mm. (average approximately 2.75), of female 2.55-3.13 mm. (average approximately 2.86); color varying, sometimes wholly black but usually ranging from head and mesosoma black, metasoma black but for two basal fulvous segments, to color as described for *N. n. nevadensis*; wings of female hyaline-yellow to darkly infusate; pubescence of mesonotum, fasciae and sterna of females white to rufescent; appressed hairs on discs of terga one to five of female absent or very sparse; face short, clypeus not almost covering folded mandibles, average ratio of facial length to facial width of male 1:1.17, of female 1:1.25.

This form is easily distinguished from *N. n. bakeri* by its smaller size, more coarse and sparse punctation, and by the shape of the rugose propodeal base, which is narrowly crescent-shaped. Moreover, in areas where the two might be confused, *arizonensis* is usually mostly red, whereas *bakeri* is usually mostly black. *N. n. arizonensis* is separated from *N. n. stellata* by the absence of appressed tergal pubescence in the female of the former, and by the sharp proximal tooth of the male hind tibia. The black specimens are difficult to distinguish from *N. n. angelesia*, their smaller size being the best criterion.

Variation: Cockerell (1899, 1910) applied the species name *arizonensis* to a series of wholly black specimens labelled "Tucson, Arizona" or "Arizona." The same author (1925) reclassified the form as a black subspecies of *N. nevadensis*. Since forms with varying amounts of red as well as wholly black forms are recorded from the same localities over a wide area (and are, in fact usually predominant over the black forms), there seems to be little reason for restricting the name to the black specimens alone. It might be supposed that the different color forms are sympatric species, but the evidence does not support such a conclusion.

The fact that an almost complete series of intergrades exists between black and red indicates that interbreeding probably occurs. Moreover, all attempts to separate red from black forms by morpho-

logical differences, by host plants visited, and by seasons of activity have been unsuccessful. A difference of means test, using the width of face measurement was applied to red and black females from Tucson, Arizona, and Blythe, California. In both localities, results showed no significant differences between the two color forms ($P > .05$) indicating that in each locality, they are members of a single population on the basis of the character tested. Further evidence concerning the status of these color forms is found at their nesting sites. In 1951, Dr. G. E. Bohart and the author found black and partially red bees nesting together in a site near Delta, Utah, and this same observation has been reported separately by Dr. E. G. Linsley (in litt.) for a population at Blythe, California, and by Dr. G. D. Butler (in litt.) at Roll, Arizona. On the basis of the above facts, there is little doubt that the color forms represent normal components of certain populations and that their taxonomic separation is neither natural nor desirable.

N. nevadensis arizonensis, as herein defined, includes several geographically recognizable forms. It is felt that no useful purpose would be served by their taxonomic recognition, since these forms grade imperceptibly into one another. The details of this geographic variation will be presented elsewhere.

Distribution: *N. n. arizonensis* ranges over a large area from southeastern California to eastern New Mexico and from central Utah to northern Jalisco. It forms a wide zone of intergradation with populations of *N. n. angelesia* in southern California and also appears to intergrade with *N. n. stellata* in this region. It has not been found to intergrade with *N. n. bakeri* at any point along their adjoining ranges except in western Texas (see description of *N. n. bakeri*). *N. n. arizonensis* as defined within this paper has often been mistaken for *N. nevadensis nevadensis*, with which it intergrades along the Utah-Nevada border, but the two are separable on the basis of the characters described above.

Type locality: "Arizona."

Specimens examined: ARIZONA: Ajo, Arivaca, Arlington, Ashfork, Benson, Bill Williams Fork (Mohave Co.), Carr Canyon (Huachuca Mts.), Cochise Co., Continental, Dateland, Douglas, Eloy, Fredonia, Gila Bend, Harshaw, Marinette, McNeal, Oracle, Phoenix, Red Rock, Roll, Roosevelt Lake, Sabino Canyon, San Francisco Mts. (Coconino Co.), San Simon (Cochise Co.), Sentinel, Toltec, Tombstone, Tucson, Winslow, Yuma. NEW MEXICO: Albuquerque, Bernalillo, Carlsbad, Columbus, Glenwood, Laguna, La Luz, Las

Cruces, Malaga, Mesilla Park, Portales, Roswell, Santa Fe, Santa Rosa. TEXAS: Alpine, Cornudas (Hudspeth Co.), El Paso, Ft. Hancock, Marathon, Salt Flat (Hudspeth Co.). UTAH: Delta, Jericho, Lynndyl. AGUAS CALIENTES: Rincón de Romos. CHIHUAHUA: Chihuahua, Jiménez, Parral, Samalayuca, Santa Bárbara, Villa Ahumada. COAHUILA: Cabos, Guadalupe. DURANGO: 8 mi. So. Canutillo, Durango, Nombre de Dios, San Juan del Río. JALISCO: San Juan de los Lagos. ZACATECAS: Sain Alto.

Total number of specimens examined: 201 males, 277 females. The majority of these were taken between July 15 and Aug. 21. Males have been reported as early as May 6 and females as late as Sept. 22.

Flower records: *Asclepias* spp., 1 ♀; *Baccharis glutinosa*, 6 ♀; *Chrysothamnus* spp., 1 ♀; *Cleome serrulata*, 1 ♂; *Eriogonum* spp., 1 ♀; *Euphorbia* spp., 1 ♂, 1 ♀; *Eysenhardtia polystachya*, 2 ♂, 1 ♀; *Grindelia squarrosa*, 3 ♂, 40 ♀; *Grindelia* spp., *Guardiola tulocarpa*, 5 ♂, 3 ♀; *Gutierrezia* spp., 1 ♀; *Haplopappus spinulosus*, 5 ♀; *Helianthus* spp., 2 ♂; *Hymenothrix wislizeni*, 1 ♀; *Hymenoxys* spp., 3 ♀; *Isocoma heterophylla*, 1 ♂; *Lygodesmia juncea*, 1 ♂, 2 ♀; *Pectis papposa*, 3 ♂, 5 ♀; *Psilotrophe cooperi*, 1 ♀; *Solanum elaeagnifolium*, 4 ♂; *Solanum* spp., 1 ♂; *Sphaeralcea* spp., 1 ♂; *Verbesina* spp., 2 ♂; *Wislizenia refracta*, 1 ♀.

Nomia (Epinomia) nevadensis angelesia Cockerell

(Fig. 2)

Nomia arizonensis angelesia Cockerell, 1910, Proc. U. S. Nat. Mus., vol. 38, p. 293.

Nomia nevadensis angelesia Cockerell, 1925, Pan-Pac. Ent., vol. 1, p. 179.

Description: As described for *N. nevadensis nevadensis* except as follows:

Width of face of male 2.62-3.30 mm. (average approximately 2.99), of female 2.79-3.37 (average 3.10); color wholly black, wings honey brown, moderately infuscated; pubescence of mesonotum long, buffy white, that of fasciae and sternal hairs also buffy white; appressed hairs on discs of terga one to five of female absent or very sparse; face short, clypeus not almost covering folded mandibles, average ratio of facial width of male 1:1.17, of female 1:1.23.

This subspecies is separable from the red forms of *nevadensis arizonensis* by color and by its larger size and longer mesonotal pubescence. It is difficult to distinguish from black forms of the latter in the more southern parts of its range, but is larger than

arizonensis in the more northern parts of its range. It differs from *N. n. stellata* by being larger, by the absence of appressed tergal pubescence in the female, and by the presence of a sharp median tooth on the hind tibia of the male.

Distribution: *N. n. angelesia* is found from southern Oregon to the northern coast of Baja California, and east to west central Nevada and south central California. There is a wide zone of intergradation with *arizonensis* in the latter area, but no intergrades with *stellata* have been found.

Type locality: Los Angeles County, California.

Specimens examined: CALIFORNIA: Antioch, Berkeley, Blythe, Coachella, Davis, Dos Palos, Dulzura, Firebaugh, Hagerman Park, Helendale (San Bernardino Co.), Hemet, Hot Creek (Mono Co.), Imperial Co., Indio, Jacumba, Kane Springs (Imperial Co.), Los Angeles, Mammoth Lakes (Mono Co.), Mendota, Newport Beach (Orange Co.), Oakley, Palo Verde, Rialto, Rio Vista, Riverside, Sacramento, San Diego, San Diego Co., San Jacinto, Tulare, Turlock, Vina, Yucca Valley. NEVADA: Walker Lake (Mineral Co.). OREGON: Diamond Lake (Douglas Co.). BAJA CALIFORNIA: 35 mi. south of Tijuana.

Total number of specimens examined: 205 males, 194 females. The majority of these specimens were taken between July 10 and Aug. 28. Throughout the range of the form, however, the flight season is long (April 20-Oct. 26) and it seems probable that there is commonly more than one generation per year.

Flower records: *Aster spinosa*, 3 ♀; *Brassica* spp., 2 ♂; *Centromadia pungens*, 6 ♂, 6 ♀; *Chrysothamnus* spp., 1 ♂; Compositae (no further data given), 24 ♂; *Croton californicus*, 4 ♂; Cruciferae (no further data given), 3 ♂; *Grindelia camporum*, 1 ♀; *Grindelia* spp., 2 ♂, 10 ♀; *Gutierrezia sarothrae*, 7 ♂, 13 ♀; *Heterotheca grandiflora*, 3 ♀; *Isocoma* spp., 2 ♀; *Lotus americana*, 4 ♂; *Medicago sativa*, 8 ♂; *Melilotus alba*, 11 ♂, 2 ♀; *Melilotus* spp., 11 ♂, 5 ♀; *Pectis papposa*, 4 ♂, 19 ♀; *Solidago occidentalis*, 1 ♂; *Solidago* spp., 3 ♂, 22 ♀; *Tamarix gallica*, 1 ♂, 1 ♀; *Trichostema* spp., 1 ♀; *Wislizenia refracta*, 1 ♂.

Nomia (Epinomia) nevadensis stellata, subsp. nov.

(Figs. 2; 4G)

Description: As described for *N. n. nevadensis* except as follows:

Male: Smaller, width of face 2.82 mm. (2.45-2.82); color wholly black (to head and mesosoma black, two basal metasomal segments fulvo-ferruginous); wings hyaline-brown; median excavation of hind tibia shallow (fig. 4, G), prominence formed by its proximal margin

rounded rather than angulate (or excavation deeper, prominence angulate); under surfaces of middle and hind tibiae shallowly undulate (or smooth); face shorter, clypeus not almost covering folded mandibles, average ratio of facial length to facial width 1:1.16.

Female: Smaller, width of face 2.79 mm. (2.55-2.89); head, mesosoma, legs, and lateral portions of metasomal terga black, discs of metasomal terga dull fulvo-ferruginous (or wholly black); wings hyaline-brown; pubescence of mesonotum and fasciae pale buffy white; discs of metasomal terga more densely covered with short, plumose, appressed hairs, most prominent on terga three and four, stiff, posteriorly directed hairs basad of fasciae inconspicuous; long hairs of sterna two to five uniformly buffy white; posterior margin of horizontal rugose base of propodeum carinate (or this carina lacking); face short, clypeus not almost covering folded mandibles, average ratio of facial length to facial width approximately 1:1.22.

N. n. stellata differs from *N. n. angelesia* in being smaller with much lighter wings. It may be separated from *N. n. arizonensis*, as well as from *angelesia* by the presence of the appressed pubescence on the metasomal terga, the carinate posterior margin of the propodeal base in the female, and by the absence of the sharp median tooth on the hind tibia of the male (fig. 4, G).

Variation: Due, perhaps, to its occurrence on a narrow peninsula, this form shows a wide range of intrapopulational variation. Males overlap in every key character with those of *arizonensis* and are only partially separable from that form. Females are distinct from those of surrounding subspecies. Moreover, marked differences in color occur between the sexes, males usually being wholly black while females often possess one or more red terga.

Since the males can be referred to adjoining forms, the author has preferred to designate this form as a subspecies, being aware that later research may prove it to be a distinct species.

Distribution: Middle Baja California north to the southern portions of California. Male specimens from Imperial Co., California, were examined which are believed to be intergrades between this form and *N. n. arizonensis*. No evidence of intergradation with *N. n. angelesia* in northwestern Baja California has been found.

Type material: Holotype male, allotype female, ten male and ten female paratypes from San Pedro, Baja California, Oct. 4, 1941 (E. S. Ross, G. E. Bohart).

Type repositories: Holotype, allotype, four male and four female paratypes in the California Academy of Sciences. One male and one female paratype in the Snow Entomological Museum.

Specimens examined: BAJA CALIFORNIA: 15 mi. So. San Domingo, Oct. 4, 1941 (E. S. Ross, G. E. Bohart), 2 ♂; San Pedro, Oct. 7, 1941 (E. S. Ross, G. E. Bohart), 13 ♂, 15 ♀, plus type material.

Nomia (Epinomia) nevadensis bakeri Cockerell

(Figs. 2; 3M)

Nomia bakeri Cockerell, 1898, Entomologist, vol. 31, p. 32.

Nomia pattoni Cockerell, 1910, Proc. U. S. Nat. Mus., vol. 38, p. 292.

Nomia nevadensis pattoni, Cockerell and Blair, 1930, Amer. Mus. Novitates, no. 433, pp. 14, 16.

Nomia bakeri var. *rufbasis* Cockerell, 1930. In Cockerell and Blair, Amer. Mus. Novitates, no. 433, p. 14.

Nomia nevadensis bakeri, Cockerell and Blair, 1930, Amer. Mus. Novitates, no. 433, pp. 7, 14, 16.

Description: As described for *N. n. nevadensis* except as follows:

Male: Width of face 2.41-3.13 mm. (average approximately 2.99 mm.); color varying, rarely as described for *N. n. nevadensis*, usually ranging from wholly black to head and mesosoma black, metasoma black but for two ferruginous basal segments; apex of hind femur usually black, remaining segments of leg fulvous; wings honey brown to moderately infuscated; punctures of vertex finer and closer than those of clypeus, punctation finer and closer throughout than that described for *N. n. nevadensis*; horizontal rugose base of propodeum widely crescent shaped or appearing truncate posteriorly; face shorter than that described for *nevadensis*, clypeus not almost covering folded mandibles, average ratio of facial length to facial width, 1:1.17.

Female: Width of face 2.75-3.30 mm. (average approximately 3.06 mm.); color as described for male; wings moderately to heavily infuscated; pubescence of mesonotum white to buffy white; hairs of metasomal sterna buffy white; appressed hairs on discs of terga one to five absent, stiff, posteriorly directed hairs basad of fasciae inconspicuous; punctures of first and second metasomal terga nearly alike, punctation finer and closer throughout than that described for *N. n. nevadensis*; rugose propodeal base as described above for male; face short, clypeus not almost covering mandibles, average ratio of facial length to facial width 1:1.28.

This subspecies is easily distinguishable from *N. n. arizonensis* by its larger size, finer and closer punctation, and by the widely crescentic or truncate configuration of the rugose propodeal base. In areas where the two meet, *bakeri* is usually wholly or largely black while *arizonensis* usually possesses at least two fulvous metasomal segments.

Variation: *N. n. bakeri* is usually readily separable from all other subspecies of *N. nevadensis* on the basis of the characters given

above, and was considered as a distinct species until Cockerell and Blair (1930) placed it under *N. nevadensis* because of similarities in the male genitalia of the two forms.

Despite the differences mentioned in the description, the genitalia and hind tibiae of the males agree with those of *N. n. arizonensis*, which it neighbors to the east. These two characters have been especially useful in separating the species of *Epinomia*. Moreover, neither the size nor color differences between *bakeri* and other subspecies of *nevadensis* are extraordinary. The largest *bakeri* are no larger than northern California specimens of *N. n. angelesia*, and in the southern part of its range, fulvous *bakeri* are found which closely resemble other red forms of the species.

As stated previously, *N. n. bakeri* geographically replaces *arizonensis* to the east. However, the status of these bees where their ranges meet is obscure and requires further investigation. Cockerell (1930) thought of *bakeri* only as a plains bee and suggested that it might intergrade with *arizonensis* in southeastern Colorado. Because specimens from this area were not available for purposes of the present paper, the truth of this surmise is still untested. A single typical specimen of *bakeri* from each of two localities in western Colorado (Durango and Leadville) indicates, however, that this form is established west of the Rocky Mountains. Since typical *arizonensis* is known from Albuquerque, if intergradation does take place in this area, it must occur between the latter locality and Durango. Along the eastern border of New Mexico, there is evidence suggesting that the two ranges overlap. A single small male *bakeri* from Tucumcari, New Mexico, has been examined, and a single typical male *arizonensis* is known from Portales, New Mexico, southwest of Tucumcari.

From Barstow, Ward County, Texas, however, comes a series of fulvous bees which seem to be intergrades between the two forms. On the basis of this evidence, *bakeri* is placed as a subspecies of *nevadensis*. It is clear, however, that more study and material is needed before the status of these forms is settled.

Distribution: Northern Florida to south central Wyoming, the eastern two thirds of Colorado, and the extreme northern and eastern portions of New Mexico south to near Barstow, Texas, thence southeast to the gulf coast near Matamoros, Tamaulipas.

Type locality: "Colorado."

Specimens examined: ALABAMA: Selma. COLORADO: Berkeley, Boulder, Canfield, Crook, Crowley, Denver, Durango, Ft. Lupton, La Junta, Lamar, Leadville, Limon, Logan Co., Roggen, Sterling,

White Rock, Valmont. FLORIDA: Flagler Beach. KANSAS: Douglas Co., Garden City, Hutchinson, Lakin, Newton, Pawnee Co., Pierceville, St. John, Stafford. LOUISIANA: Tallulah. MISSISSIPPI: Hattiesburg. NEBRASKA: Mitchell. NEW MEXICO: Tucumcari. TEXAS: Barstow, Bishop, Conlen, Cotulla, Dalhart, Dilley. WYOMING: Guernsey, Lingle. TAMAULIPAS: Matamoros.

Total number of specimens examined: 110 males, 232 females. The majority of these were taken between July 21 and Aug. 30. Males have been taken as early as April 17 and females as late as Oct. 15. There are probably several generations per year in the southern portions of the range.

Flower Records: *Bidens involucrata*, 3 ♂; *Boltonia asteroides*, 2 ♂; *Chrysopsis microcephala*, 2 ♀; *Chrysopsis* spp., 1 ♀; *Coreopsis* spp., 3 ♂, 1 ♀; *Dalea lanata*, 2 ♂; *Grindelia* spp., 5 ♂; *Heterotheca* spp., 2 ♂, 42 ♀; *Isopappus* sp., 2 ♂, 15 ♂; *Melilotus alba*, 8 ♂, 1 ♀; *Prionopsis* spp., 2 ♀; *Prosopis* spp., 2 ♀; *Solidago* spp., 3 ♀; *Thelaspisma gracile*, 1 ♂; *Verbesina* spp., 1 ♂.

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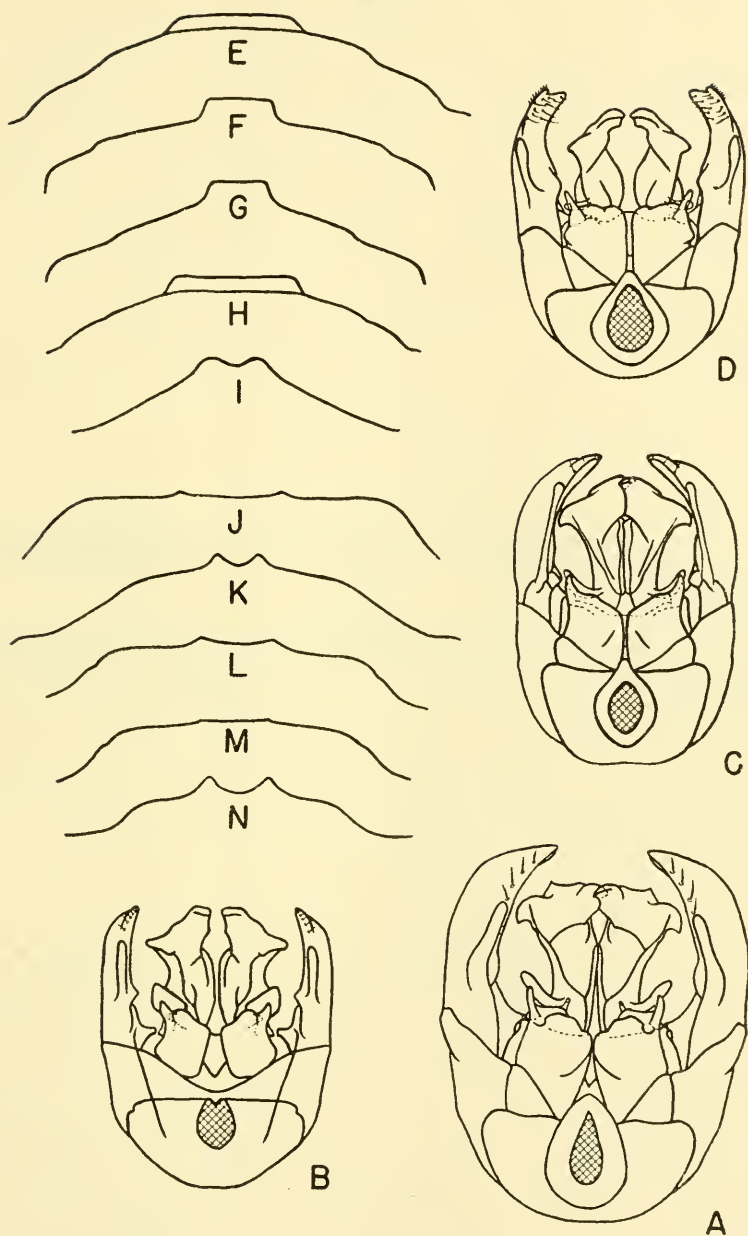
A-D. Genital capsules of *Epinomia*, ventral aspect.

A. *N. triangulifera* (Amazonia, Mo.); B. *N. micheneri* (Carr Canyon, Ariz., paratype); C. *N. nevadensis nevadensis* (Fairbanks Springs, Nev.); D. *N. boharti* (paratype).

E.-N. Clypeal margins of *Epinomia* as seen from beneath.

E. *N. triangulifera*, male (Douglas Co., Kans.); F. *N. micheneri* (holotype); G. *N. micheneri* (Carr Canyon, Ariz.), (male paratype); H. *N. nevadensis nevadensis*, male (Fairbanks Springs, Nev.); I. *N. boharti* (male paratype); J. *N. triangulifera*, female (Lawrence, Kans.); K. *N. micheneri* (allotype); L. *N. nevadensis arizonensis*, female (Delta, Utah); M. *N. nevadensis bakeri*, female (La Junta, Colo.); N. *N. boharti*, female (San Blas, Nayarit).

FIG. 3



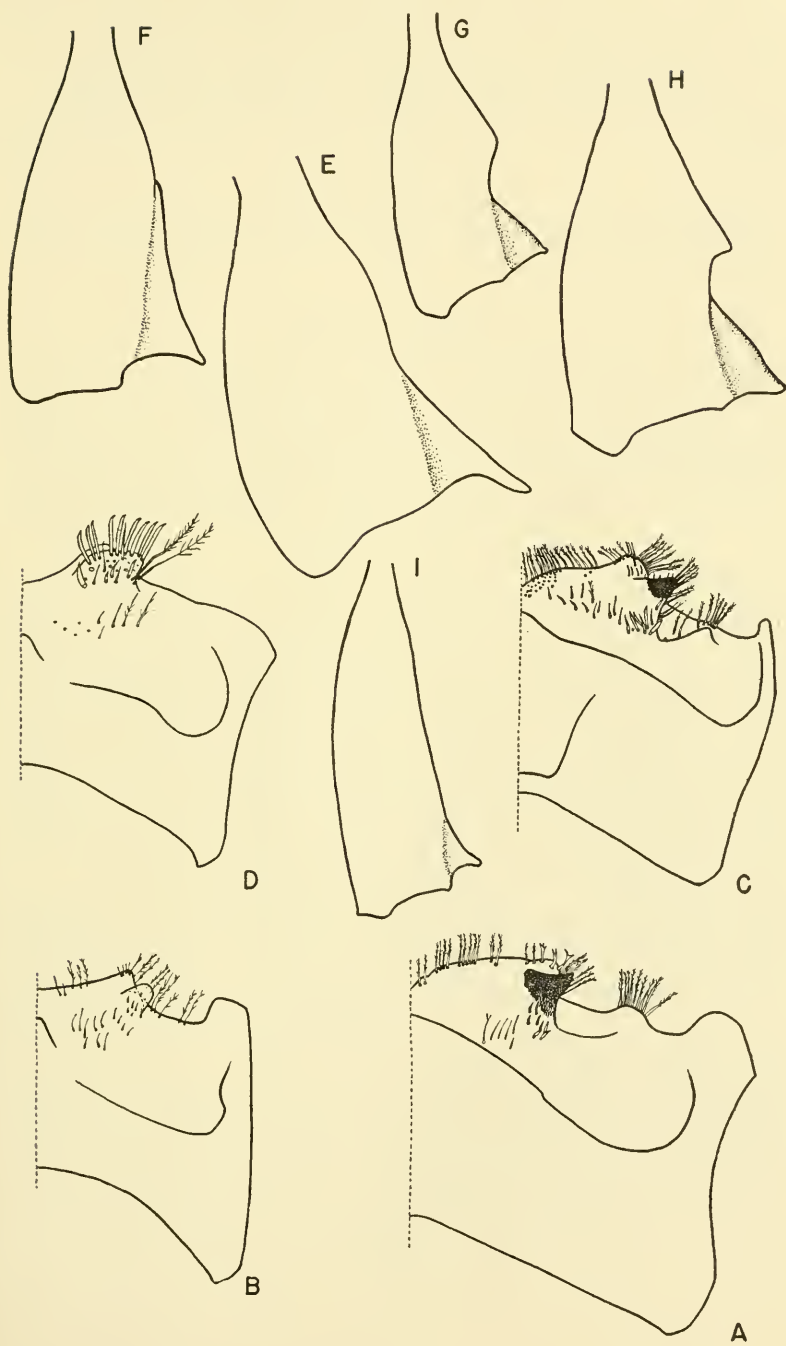
A-D. Sterna five of male *Epinomia*.

A. *N. triangulifera* (Lawrence, Kans.); B. *N. micheneri* (Sta. Bárbara, Chihuahua); C. *N. nevadensis nevadensis* (Fairbanks Springs,, Nev.); D. *N. boharti* (paratype).

E-I. Right hind tibiae of male *Epinomia*.

E. *N. triangulifera* (Promontory, Utah); F. *N. micheneri* (holotype); G. *N. nevadensis stellata* (paratype); H. *N. nevadensis nevadensis* (lectotype); I. *N. boharti* (paratype).

FIG. 4



THE UNIVERSITY OF KANSAS SCIENCE BULLETIN

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[No. 17

The Status of the Mexican Lizards of the Genus *Mabuya*

BY

ROBERT G. WEBB *

ABSTRACT. The Mexican lizards of the genus *Mabuya* are examined critically. Material consisting of 75 specimens from seven Mexican states was available. A study of the variation from the various localities was made and it was found that the populations were for the most part homogeneous and no subspecific variants were recognized. It was determined that the proper name for the Mexican species is *Mabuya brachypoda* Taylor.

INTRODUCTION

The conservatism of Dunn (1936), who considered *Mabuya mabouya mabouya* as ranging from Mexico to Ecuador, Brazil and the Lesser Antilles has been questioned. Burger (1952) revived the name *alliacea* of Cope (1876) and regarded the mabuyas ranging from Mexico to Costa Rica as *Mabuya mabouya alliacea*. In addition, Taylor (1957) resolved Costa Rican material into three distinct species, *Mabuya unimarginata*, *Mabuya brachypoda*, and *Mabuya alliacea*. Dunn, himself, (*loc. cit.*: 545) in his concept of *M. mabouya mabouya*, recognized that the populations were ". . . numerous and quite diverse, . . ." This variation in populations of the mainland coupled with an insular type locality (restricted to St. Vincent by Smith and Taylor, 1950:156) for *M. mabouya mabouya* suggests the presence of mainland populations worthy of taxonomic recognition.

In view of this variation, Dr. Edward H. Taylor suggested to the author that a study of the variation exhibited by the genus *Mabuya* in Mexico be made in an effort to clarify the taxonomic relationships of the northern mainland populations. The author is grateful to Doctor Taylor for permission to study specimens in

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his private collection and for constructive criticism of the manuscript.

The present study is based on an examination of 75 specimens from seven Mexican states which were collected intermittently in the years 1932 to 1940. All numbers are those of the EHT-HMS collection (private collection of E. H. Taylor), and are listed by locality below.

Campeche.—Balchacaj, 14435-36, 14438-39, 14450-51, 14457; Tres Brazos, 14441-45, 14447-48; Encarnación, 14453-54, 14456 (17 specimens).

Chiapas.—San Ricardo, 10504; Libertad, 15425; Tuxtla Gutierrez, 15343 (3 specimens).

Guerrero.—12 mi. S. Chilpancingo, 10453; 7 mi. E. Chilpancingo, 22237-38, 23915; near Chilpancingo, 23885; 1 mi. N. Organos, 10454; El Limoncito, near Acapulco, 19094-95, 19097-98, 19100-01, 19103-04, 19106-07; between Chilpancingo and Omilteme, 23882-83; Agua del Obispo, 10456-57, 23907-08 (22 specimens).

Michoacán.—Uruapan, 10460, 10462-63, 10465-66, 10468-69, 10471-72, 10474-75, 10477-78, 10480-81, 10483-84, 10486-87, 10489-90, 10492-93, 10495-96, 10498-99, 10501-02 (29 specimens).

Morelos.—Puente de Ixtla, 19092 (1 specimen).

Oaxaca.—Totalapan, 10459 (1 specimen).

Yucatán.—Progreso, 14432; Mérida, 14433 (2 specimens).

VARIATION

Body proportions.—The following measurements were utilized:

Snout-vent length—from the tip of the snout to the anterior margin of the anus.

Tail length—from the anterior margin of the anus to the tip of the tail; only measurements of complete tails were taken.

Head length—from tip of snout to anterior margin of ear along a line parallel to the lateral axis of the head.

Head width—the greatest width in a transverse straight line.

Leg length—from the tip of the longest toe (including the claw) to the angle with the body (posterior to fore limb and anterior to hind limb), with the leg extended at right angles to the body.

Axilla-groin distance—a straight line from the posterior margin of insertion of the fore limb to the anterior margin of the insertion of the hind limb.

Also, ratios from six body proportions were calculated; these were snout-vent/axilla-groin, snout-vent/fore limb, snout-vent/hind limb,

snout-vent/head length, snout-vent/head width, and axilla-groin/hind limb.

In an attempt to determine ontogenetic variation, individuals were assigned to three arbitrary size groups as follows: 1) 20-40 mm., 2) 41-60 mm., 3) 61-83 mm.

The largest sample available from a single locality is 29 specimens from Uruapan, Michoacán. A consideration of geographic variation involved a comparison of the Michoacán sample with 22 specimens from Guerrero and 19 from Campeche.

The construction of scattergrams and calculation of mean and extreme ratios revealed little sexual dimorphism, ontogenetic growth, or geographic variation in body measurements. Smaller individuals have larger heads. In the 20-40 mm. size-group the head length is contained in the snout-vent length an average of 4.2 times (13 specimens), whereas in the 61-83 mm. size-group it is contained 5.3 times (38 specimens). Similarly, the snout-vent/head width average ratio for 13 specimens in the 20-40 mm. size-group averages 6.2, whereas the same for 38 specimens in the 61-83 mm. size-group averages 7.4.

The hind limb is longer in the smaller individuals in relation to the axilla-groin length. The average axilla-groin/hind leg ratio in the 20-40 mm. size-group was 1.4, whereas the same in the 61-83 mm. size-group was 1.7. The length of the fore limb in relation to the axilla-groin length was not considered. It is of interest that no ontogenetic growth in the hind limb is revealed if a comparison of the snout-vent/hind limb ratios of the three size-groups is made, as an average ratio of 3.1 is maintained; this is probably reflected in the differential growth of the head.

In regard to tail length, seven juveniles ranging in snout-vent length from 26 to 31 mm. (sex undetermined) have an average tail length/snout-vent length ratio of 1.3 (1.2-1.4). The analysis of variation in tail length of adults was limited to five specimens (2 males, 3 females) in which the tail length/snout-vent ratios in males (1.9 and 2.0) are larger than that in females (1.7, 1.7, and 1.7). A male, 64 mm. in snout-vent length, had the longest tail, (130 mm.); all females exceeded 64 mm. in snout-vent length. The meager data indicate that adult males have longer tails in relation to snout-vent length than do adult females.

Females attain a larger size than males and have an average snout-vent length of 71.2 mm. (extremes 62-83 mm.) based on 19 specimens, whereas males have an average snout-vent length of

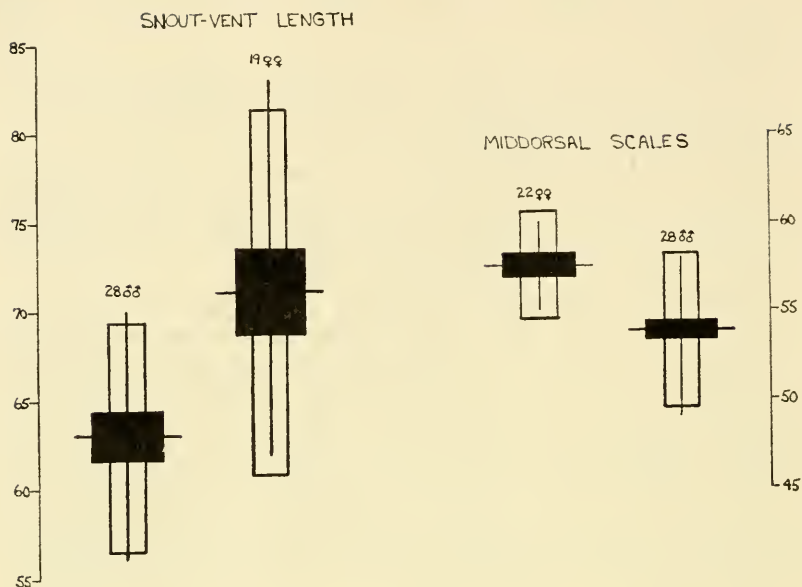


FIG. 1. Variation between sexes in snout-vent length and number of middorsal scales. The horizontal line indicates the mean; the vertical line, the observed variation; the white rectangle, four standard deviations; the black rectangle, four standard errors of the mean.

63.0 mm. (extremes 56-70 mm.) based on 28 specimens (Fig. 1). Data used are from specimens regarded as sexually mature (see page 1312).

Scutellation.—The dorsal body scales of all specimens are smooth with no evidence of keels.

Middorsal scales: A count of the dorsal scales from the most anterior body scale (excluding the nuchal), in a straight line at or near the middorsal line as far back as a line even with the posterior margins of the thighs, when the hind legs are held at right angles to the body. There is a distinct sexual dimorphism in the number of middorsal scales (Fig. 1). Males averaged 53.9 (extremes 49-58), based on 28 individuals, whereas females averaged 57.6 (extremes 55-60), based on 22 individuals.

Mid-body scales: A transverse count of the longitudinal scalerows at a point one fourth the axilla-groin length anterior to the insertion of the hind leg. Counts taken at mid-body usually include intercalary rows which extend posteriorly from the axillary region. These scales varied in number from 28 to 32. A count of 28 scale-rows (51%) was recorded for 29 of 57 specimens; thirty scalerows

occurred in 24 counts (42%) and 32 scalerows in 4 counts (7%). The count of 32 scalerows was restricted to females.

Supralabials: The scales bordering the upper edge of the mouth except at the tip of the snout where the rostral occurs. The largest posterior scale is regarded as the last supralabial. Of 73 specimens in which both sides could be counted, 51 (70%) had a combination of 6-6, 15 (20%) had a combination of 6-7, 5 (7%) had a combination of 5-6, and 2 specimens (3%) had a combination of 7-7. Considering each side separately and based on 148 counts, 6 supralabials occurred in 124 counts (84%), 7 occurred in 19 counts (13%), and 5 occurred in 5 counts (3%). When a count of 6-6 occurs, the fifth supralabial is the largest and lies immediately beneath the orbit, with one labial posterior and four anterior. In the case of seven supralabials, the sixth is the largest and beneath the orbit, and with five supralabials, the fourth is the largest and beneath the orbit. Five supralabials occurred only in certain specimens from Guerrero.

Infralabials: The scales bordering the lower edge of the mouth except for the most anterior mental scale. Of 71 specimens in which both sides could be counted, 59 specimens (84%) had a combination of 6-6, 7 (9%) had a combination of 6-7, 3 (4%) had a combination of 7-7, and 2 (2%) had a combination of 5-6. Considering each side separately and based on 146 counts, six infralabials occurred in 129 counts (89%), 7 occurred in 15 counts (10%), and 5 occurred in 2 counts (1%). All specimens with five infralabials are from Guerrero.

Postmental: A scale following the mental along the midventral line. The postmental was unpaired in 72 specimens and asymmetrically divided in another.

Nuchals: The enlarged paired scales immediately posterior to the parietals. Of 72 specimens, all had one pair of nuchals; the two nuchals were fused medially in one specimen from Yucatán.

Parietals: Paired scales posterior to the frontoparietals and bordering the interparietal on either side. Of 73 specimens, all had the parietals in contact posteriorly.

Supraoculars: The scales above the orbits. A count of 4-4 occurred in 68 specimens (95%), two specimens had a count of 3-4 (3%), and one specimen had a count of 3-3 (2%). Considering each side separately and based on 146 counts, four supraoculars occurred in 141 counts (97%) and three supraoculars occurred in 5 counts (3%). The most anterior supraocular is the smallest, the one immediately posterior to it is the largest.

Prefrontals: Paired scales immediately preceding the frontal. The prefrontals were separated in 67 specimens (92%) and in contact in six specimens (8%).

Supranasals: Paired scales immediately preceding the frontonasal and posterior to the rostral. Of 75 specimens, 55 (73%) had the supranasals in contact medially, whereas they were separated in 20 specimens (27%). Of possible geographic interest is the fact that none of the 28 specimens from Michoacán had the supranasals separated. Dunn (*loc. cit.* :540) reports contact of the supranasals in only 33% of the specimens he examined from Mexico. Burger's comments (*loc. cit.* :187) concerning the variation of this character in Mexico closely parallels the results of this study.

Chin shields: A paired series of scales extending posteriorly from the postmental. From a total of 73 specimens, 52 (71%) had a combination of 2-2, 10 (14%) had a combination of 1-2, 8 (11%) had a combination of 1-1, 2 (3%) had a combination of 2-3, and 1 specimen (1%) had a combination of 3-3.

Coloration.—The following comments pertain to all sizes of both sexes, there being little or no sexual or ontogenetic variation in coloration. Dorsally the ground color ranges from a dark olive to a light burnt-brown and may be uniform or marked with small dark spots. The venter, throat, and undersurface of the limbs are light and without markings. The anterior, posterior, and dorsal surfaces of the limbs have a marbled or reticulate appearance. A lateral white stripe extends from the angle of the mouth posteriorly through the lower half of the tympanic cavity and just above the insertion of the fore limb to terminate just above the insertion of the hind limb or just posterior to it on the tail. This bilateral white stripe is about one scale wide and, at mid-body, usually (73%) overlaps two longitudinal scalerows, the ventral half of the seventh and dorsal half of the eighth scalerows on the right side, and the ventral half of the sixth and dorsal half of the seventh scalerows on the left side (excluding the middorsal scalerow). Occasionally (27%), the lateral white stripe engages only one scale row on each side, the seventh on the right and the sixth on the left. Immediately dorsal to the lateral white stripe is a longitudinal dark brown band on either side which is two (rarely one and one-half or two and one-half) scalerows wide; it begins anteriorly on the lateral head scales and extends posteriorly through the eye, the upper half of the tympanic cavity and terminates posteriorly at the posterior insertion of the hind limb. Ventral to the lateral white

stripe on both sides is a dark band varying in width, which merges with the immaculate venter. Adjacent and dorsal to the lateral brown band on either side is a narrow light line which may be indistinct.

Geographic variation and sexual differences were noted in the extent of markings on the dorsum. In males from Guerrero, Oaxaca and Morelos, the dorsum (area between lateral dark brown bands) was uniform without markings (19092, 19098, 10459), or with only a few small scattered black spots (19095, 22238, 23882). One specimen, however, (10457) had considerable dark marking. In males from Michoacán, the dorsum is more consistently marked with small black marks which in some tend to form short narrow longitudinal stripes (10465, 10483, 10498); others have a more or less uniform dorsum (10466, 10492-93). The tendency to form longitudinal dark stripes by fusion of the small black spots is increased in the more eastern states of Campeche, Chiapas and Yucatán, and is apparent in three males (14456, 14442, 14445). Another (14432) has a spotted dorsum but no evident stripes. All other males have some markings, though sparse. Females have for the most part a uniform dorsum and do not exhibit as strong a geographic trend as do males. Guerrero and Michoacán females may have a uniform dorsum or one with scattered dark marks. One female from Michoacán (22237) is strongly marked but there is no tendency for longitudinal stripes. Of 11 females from Chiapas, all have a uniform dorsum, or nearly so, except three specimens, one of which has narrow longitudinal stripes (14439), and two (14435, 15343) which tend toward the formation of longitudinal stripes.

One of Burger's criteria (*loc. cit.* :186) for recognizing the population occurring from Mexico to Costa Rica is based on the narrow dorsolateral dark stripe which is two or less scales in width rather than two and one-half or three scales. The dorsolateral dark stripes are the same as the lateral bands referred to in this paper, which are two scales wide.

COMPARISONS

The current appellation for Mexican mabuyas is *Mabuya mabouya alliacea*. Taylor (*loc. cit.*) dealing with the Costa Rican Mabuyas re-elevated *alliacea* to specific rank but made no mention that the binomial should be applied to Mexican representatives of the genus; his redefinition of *Mabuya alliacea* affords a basis for comparison with the Mexican population. The presence of an

azygous scale between the supranasals and the unequal, transverse division of each parietal scale resulting in a separation of the parietal scales, as depicted by Cope (*loc. cit.*:pl. 6, fig. 1) in the illustration accompanying the type description, is regarded as an anomaly as neither configuration has been encountered by Taylor or myself. The other characters given by Cope in the type description are either in agreement with or encompassed by the variation in the data presented by Taylor.

In regard to the enlarged preanal scales described for the types of *alliacea*, the author agrees with the comments of Dunn (*loc. cit.*: 542) who regarded the character of no useful taxonomic significance. Taylor calls attention to an axillary pit or pocket behind the insertion of the arm. These had been overlooked by previous workers. In all the Mexican specimens examined they were well developed.

Using, then, the data given by Taylor, selected characters of *Mabuya alliacea* from Costa Rica are compared with those exhibited by the specimens from Mexico (Table 1). The range of variation in the number of mid-body scales is slightly lower in *alliacea* though an average of 28 scales is common to both. *Mabuya alliacea* differs from the Mexican specimens in that 1) the sixth supralabial subtends the orbit, 2) the rostral normally touches the frontonasal, 3) a dorsolateral dark stripe is present, and 4)

TABLE 1.—Comparison of Characters of *Mabuya alliacea*, *Mabuya brachypoda* and specimens from Mexico.

	<i>alliacea</i> 18	<i>brachypoda</i> 12	Mexican specimens 75
midbody scales	26-29 28 (59%)	28-32 30 (66%)	28-32 28 (51%)
supralabial below eye	6th (84%)	5th (92%)	5th (84%)
supranasals in contact	no (82%)	yes (50%)	yes (73%)
dorsolateral dark stripe	yes	no	no
axillary pit	reduced	well defined	well defined

axillary pits are reduced and not prominent. The characters mentioned above from which the Mexican specimens differ from *alliacea* are in agreement with those mentioned by Taylor for *Mabuya brachypoda* (Table 1).

Mabuya brachypoda was described by Taylor as having limbs which, when adpressed, fail to overlap by a distance equal to or greater than the length of the hand. The limbs of the 12 speci-

mens which formed the type series were examined by the author. The separation of the adpressed limbs in Nos. 31312 and 31313 was about 5 mm. However in No. 34326 the limbs were found to overlap when adpressed. Doctor Taylor concurs with this measurement. This latter specimen has the parietals in contact and the sixth supralabial is below the eye, two characters which do not occur in the type or other paratypes. This is definitely aberrant or through some metathesis of data the locality is incorrect and the specimen may not belong where placed by Taylor.

The distance between adpressed limbs of the 12 *M. brachypoda*, as observed by the author, varied from approximately 10 mm. in the type specimen to 3-5 mm. Such variation could be due to the differential bending of the individual limbs, and a distance of 4-5 mm. between adpressed limbs need not be regarded as diagnostic. This is borne out by the fact that the limbs of No. 36313 do not overlap when adpressed, yet the sum of the fore and hind limb measurements exceeds the axilla-groin length by 5.5 mm. In other words, the length of limbs is not necessarily reflected in the degree of separation or overlap of adpressed limbs.

Although the limbs of every Mexican specimen were not adpressed, casual observation revealed either slight overlap or separation of the toes and fingers. The sum of the limb lengths exceeded the axilla-groin length in all but nine of the Mexican specimens, and in only four of 12 *M. brachypoda*. Axilla-groin/hind leg ratios of 10 specimens exceeding 64 mm. in snout-vent length from Costa Rica averaged 1.9, whereas that of 38 individuals from Mexico exceeding 61 mm. averaged 1.7. Although slightly shorter hind limbs in the Costa Rican specimens are suggested, the data are inconclusive, and the author, at present, regards the difference in limb length between the two populations negligible.

There are, therefore, no characters known which will certainly distinguish the Mexican mabuyas and *M. brachypoda* as described by Taylor. It is proposed that the binomial, *Mabuya brachypoda*, apply to all the mabuyas occurring from Mexico to Costa Rica. Pertinent data given in accounts by Mertens (1952:58, table 11, fig. 59) and Werler and Smith (1952:563, fig. 14) do not reveal any significant deviations from the variation as now known. The morphological geographic variation in this species does not seem to be great and is indicative that the species is a recent immigrant to Mexico from the south. *M. brachypoda* is apparently a lowland form, and in Mexico probably does not occur above an elevation of 3000 feet.

BREEDING BEHAVIOR

A macroscopic examination of the gonads and associated ducts of the Mexican specimens was undertaken in an effort to determine the size at sexual maturity and other aspects of the reproductive cycle.

Females.—Specimens were regarded as sexually mature if embryos were present in the oviducts. Ten specimens, ranging in snout-vent length from 62 to 83 mm. contained embryos and were collected between June 26 (10453) and July 28 (10477); embryo complements varied from four to six. Ovaries of these individuals were 4 mm. in length with the largest ovocytes about 1 mm. in diameter. Four specimens collected within the interim July 21-28 and exceeding 62 mm. in length, did not have embryos in the swollen and convoluted oviducts. The ovaries measured 4-5 mm. in length with the largest ovocytes 1 mm. in diameter; recent expulsion of embryos is suggested. Five specimens collected in September and exceeding 62 mm. in length agree with the four above-mentioned individuals except that developing ovocytes are larger (about 2 mm. in diameter) and more yolk is present. The oviducts of one specimen (14447), collected in September, contained five (two in the right, three in the left) small structures interpreted as unfertilized eggs, which had a diameter of 2 mm. A specimen (23915), 60 mm. in length (collection date unknown) had ovaries 2 mm. in length with one ovocyte 1 mm. in diameter; the oviducts were 1 mm. wide and slightly wrinkled, but contained two similar-sized structures (as in 14447) in the right oviduct. Two of these same structures were present in the convoluted oviducts of a specimen 56 mm. in length (14457) collected in October. Five specimens smaller than 50 mm. had ovaries measuring 4 mm. in length with ovocytes 1 mm. in diameter, but the oviducts were straight and narrow.

The data indicate that deposition of young, which varies from four to six, occurs in June and July; of 14 adult females collected from June 26 to July 28, ten contained well-developed embryos. Five adult females collected in September contained no embryos but larger developing ovocytes than those collected in June. The smallest female definitely considered sexually mature is 62 mm. in snout-vent length, although a length of 56 mm. is suggested.

Males.—Seventeen specimens ranging from 58 to 70 mm. in length, and collected in June and July had testes 5 to 8 mm. in length and 3 to 5 mm. in width. Ten specimens ranging from 59 to 70 mm. in length, and collected in August and September, had

smaller testes with dimensions of 4 to 6 mm. and 3 to 4 mm. Thus there is only a slight seasonal decrease in testes size. The smallest male examined and regarded as sexually mature (22238) is 56 mm. in length (no collection date), and has testes measuring 5 mm. in length and 3 mm. in width. One specimen (14456), 58 mm. in length and considered immature, was collected in October and had a testis measuring 3 mm. in length and 1 mm. in width; another individual (14444) collected in October and 51 mm. in length also had testes 3 mm. in length. A specimen (19106), considered sexually mature and 58 mm. in length was collected in July and had a testis 5 mm. in length and 3 mm. in width; this inconsistency in the relation of testis size to snout-vent length is suggestive of the approximate size at sexual maturity. This interpretation is questionable if a seasonal decrease in testis size is more marked in October. The size at sexual maturity is thought to be approximately 56 mm.

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[No. 18

The Integumental Anatomy of the Monarch Butterfly *Danaus plexippus* L. (Lepidoptera: Danaiidae)*

BY

PAUL R. EHRLICH **

ABSTRACT: This paper is the first section of a work on the integumental morphology, phylogeny and classification of the butterflies. The external and internal integumental anatomy of the common monarch butterfly is described and figured in detail and a descriptive terminology adopted which will be employed in the comparative work to follow.

INTRODUCTION

This is the first section of a work on the integumental morphology, phylogeny and classification of the butterflies (Papilionoidea). Despite the great popular interest in this group of insects they have been the subject of relatively little modern systematic work above the level of the generic revision. The interrelationships of the major groups are poorly understood, and some recent workers (*e. g.*, Clark, 1948) have given family rank to such obviously nonequivalent entities as the papilionids and the argynnids.

It seems apparent that a mere rearranging of the butterflies on the basis of well-studied characters such as wing venation or color pattern, or the introduction of a new phyletic arrangement and classification on the basis of one or two previously unstudied characters, would be of little significance. Therefore an attempt will be made to reconstruct the phylogeny of the group and arrive at a reasonable classification by utilizing as much published work as possible in conjunction with a study of the comparative integumental morphology. Unfortunately practical considerations will not permit simultaneous study of the characters existing in the im-

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mature forms, the visceral anatomy, the fine details of the microscopic anatomy, etc., nor of all the species or even all genera. However, it is hoped that sufficient characters and an adequate diversity of species can be studied so that major errors will be avoided.

This first section forms the basis for the comparative morphological study which is to follow. As far as could be determined this is the first detailed integumental anatomy of a butterfly. Several features of the monarch's anatomy, however, have been described and figured in varying detail by other authors (Burgess, 1880; Kellogg, 1893; Shepard, 1930).

The monarch was chosen for this study because it is common, widespread, and large. Both dried specimens and individuals preserved in Kahle's fixative were used, and these specimens were sometimes treated with chlorox or KOH. Brushes and fine forceps were used for the tedious job of removing the scales. The procedure adopted in preparation of the figures was as follows: every structure studied was examined in a minimum of two specimens, in one specimen when the drawing was prepared, and in a second when the description was written. The vast majority of the structures have been seen in four or more individuals. The simpler illustrations were prepared from the first specimen and merely checked in the second, while others, although outlined from one specimen, have been altered and adjusted after examination of additional specimens whose preparation showed certain features more clearly. The drawings were all made with the aid of an eyepiece grid to give proportions correctly.

The terminology used in this paper will be employed throughout the comparative study to follow. Most of the terms used by Michener (1952) in his study of the saturniid moth, *Eacles imperialis* (Drury), have been retained; however, the nomenclature of the male and female genitalia is that of Klots (1956).

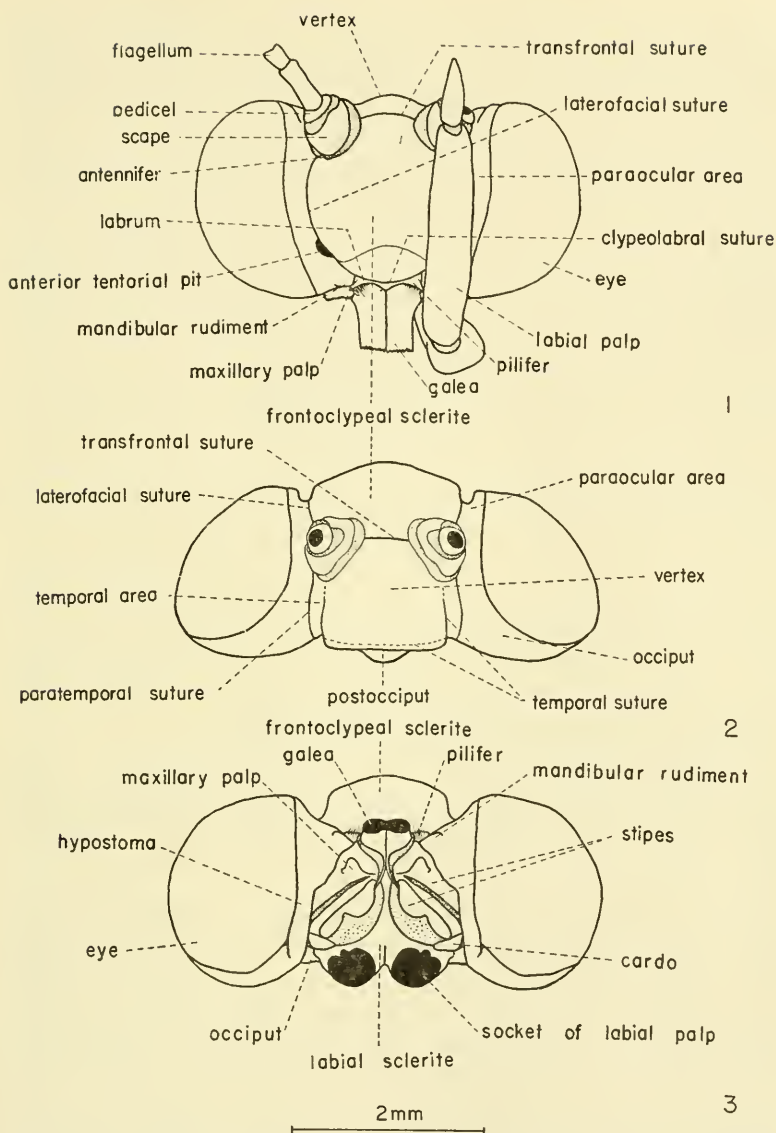
Thanks are due to Dr. C. D. Michener, Dr. K. C. Doering and Dr. Ryuichi Matsuda, all of the University of Kansas, for their aid on many facets of the work. Thanks go also to my wife, Anne H. Ehrlich, for aid in the inking of drawings and the preparation of the plates.

MORPHOLOGY

THE HEAD

(Figures 1-7)

The most prominent features of the hypognathous head are the *compound eyes*; they are approximately hemispherical and their combined width is almost one half that of the entire head. The



FIGS. 1-3. *Danaus plexippus*. 1. Front view of head. 2. Dorsal view of head. 3. Ventral view of head.

sclerites of the frontal portion of the head between the eyes are termed here, collectively, the *face*. The homologies of these sclerites are uncertain, but it seems unlikely that the terminology used by Michener (1952), which is based on that of DuPorte (1946),

reflects the true situation. The nomenclature employed here for the facial sclerites is based on DuPorte's more recent work (1956). The central area of the face is occupied by the large protuberant roughly circular *frontoclypeal sclerite*. This structure is bounded above by a sulcus connecting the inner margins of the antennal sockets, the *transfrontal suture*. This suture is only weakly in evidence externally, but is represented by a fairly strong ridge internally. Dorsolaterally the sclerite is bounded by the antennal sockets, at the edges of which it is infolded to form strong ridges along the lower parts of the sockets. These ridges connect with the ridge of the transfrontal suture and each bears on its lateral end a small dorsal projection, the *antennifer*, which is an articulation point for the scape of the antenna. Laterally the frontoclypeal sclerite is bounded by the curved *laterofacial sutures*, which contain the prominent *anterior tentorial pits* and run from the dorso-lateral edges of the labrum up to the ventral margins of the antennal sockets. These sutures, although not extremely prominent externally (they lie at the base of the forward thrust plateau of the frontoclypeal sclerite), are represented internally by large ridges which are major strengthening features of the forward wall of the head. Approximately the lower fifth of the frontoclypeal sclerite is separated from the main portion by a transverse heavily sclerotized band, designated here the *transclypeal band*.

Below the frontoclypeal sclerite and separated from it by a weak *clypeolabral suture* is a small transverse sclerite, the *labrum*. The labrum has on its ventrolateral edges cylindroconical projections called *pilifers*, each of which bears a row of bristles on its inner edge.

The anatomical facts presented by DuPorte (1956, pp. 113-114, fig. 4) have been confirmed by dissection by the present author. The validity of DuPorte's interpretation of these facts rests in large part on the answers to some of the more basic questions of insect morphology. These questions, concerning the value of musculature and innervation as morphological landmarks, the significance of the position of the anterior tentorial pits and their relationship to the so-called epistomal and frontogenal sutures, and the strictness with which interordinal homologies of facial sclerites or areas can be drawn, cannot be taken up in this paper.

The areas between the laterofacial sutures and the inner margins of the eyes are known as the *paraocular areas* (Michener, 1944). Near the ventral limit of each paraocular area, behind and slightly

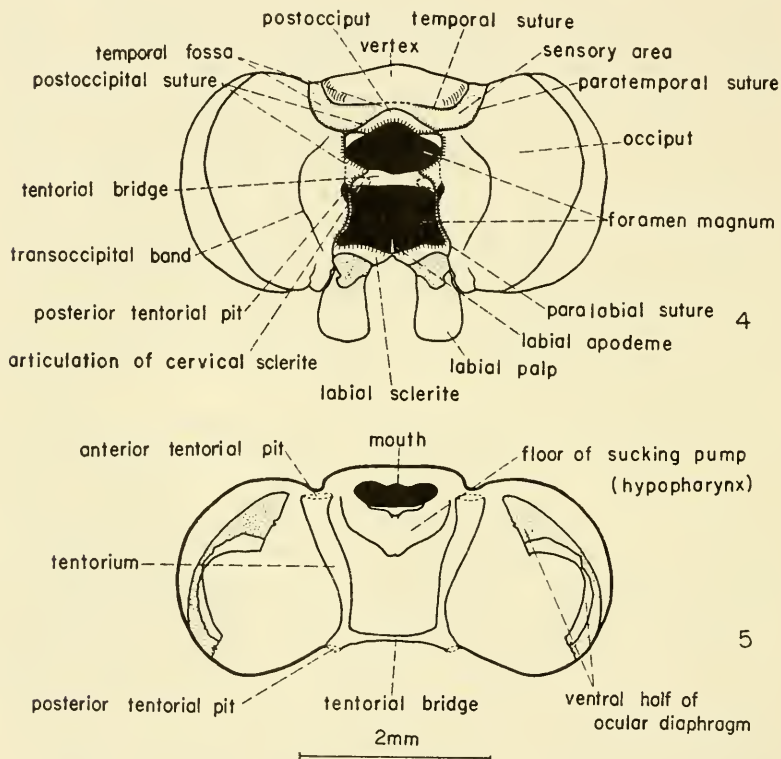
lateral to the pilifer, is a small protuberance, the *mandibular rudiment*.

The antennae, situated at the dorsolateral margins of the fronto-clypeal sclerite, are long (each being more than three times as long as the head is wide) and clubbed. The basal segment, or *scape*, of each antenna is relatively large, ringlike, and wider anteriorly than posteriorly. It has on its anterodorsal edge a small articulatory process. The second segment, or *pedicel*, is a simple ring approximately one-half the size of the scape. The remainder of the antenna is the *flagellum*, which in the monarch is composed of 43 segments. The segments increase very gradually in length, and the diameter of the antenna gradually becomes slightly greater from the proximal end to the vicinity of segment 33. In this region the width of the segments (and, of course, of the whole antenna) rapidly increases, while the length of the segments is somewhat reduced. The greatest width is reached in the vicinity of segments 39 and 40, while segments 41, 42 and 43 become progressively narrower. The resultant club is somewhat more than one sixth the length of the antenna.

The ventral surface of the head between the eyes is occupied by the *proboscidal fossa*, which is very shallow in this species. The *maxillae* occupy most of the anterior section of the fossa. Most prominent are the *galeae*, which are greatly elongated, concave mesally, and grooved together to form a tube through which liquid food is drawn by the sucking pump. Supporting the galeae, and extending laterocaudally from them, are the *stipites*, each bearing a small tubercle directly behind and slightly lateral to the galea, the *maxillary palp*. Each stipes is infolded and longitudinally divided into two sections by an area of light sclerotization (shown by heavy stippling in figure 3). The inner margins of the stipites are bilobed. Behind each stipes is a small, triangular sclerite, the *cardo*. The central and posterior parts of the fossa are occupied by the somewhat triangular *labial sclerite*, which bears caudally the large sockets of the labial palps. An invagination along the mid-line of the sclerite produces an internal ridge, the *labial apodeme*. The anterior rim of each palpal socket has two short articular processes. The anterior parts of the walls of the proboscidal fossa, lateral to the maxillae, are the *hypostomal areas*. Projecting forward from their sockets at the rear of the labial sclerite and up across the face are the large, three-segmented *labial palps*. The middle segment of

each palp is the longest; the distal one is the shortest. All segments are essentially cylindrical, but the distal one is terminally produced into a point.

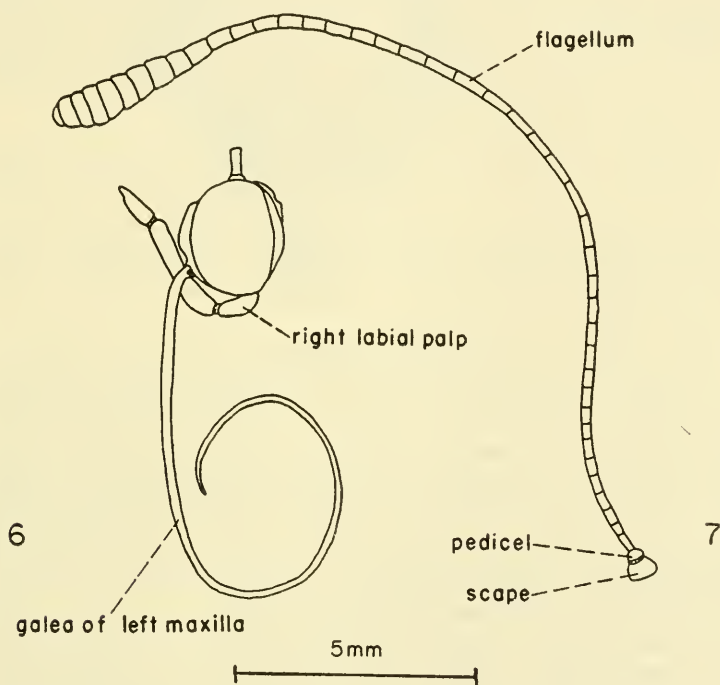
The posterior surface of the head is broken centrally by a large opening, the *foramen magnum*, which is bisected by a transverse bar, the *tentorial bridge*. At the lateral ventral corners of the bridge



FIGS. 4-5. *Danaus plexippus*. 4. Posterior view of head (the line marked by short cross lines represents attachment of cervical membrane to head). 5. Dorsal view of dissection of head to show tentorium (diagrammatic).

are two depressions, the areas of articulation of the cervical sclerites. Along its dorsal and dorsolateral margins the foramen is bordered by the *postocciput*. This sclerite is well defined dorsally by the arched *postoccipital suture*, but the suture is indistinct laterally as it runs down to the *posterior tentorial pits*. The latter portions of the suture are shown as dotted lines in figure 4. The ventral border of the foramen is the main portion of the labial sclerite behind the

sockets of the palps; the ventrolateral borders consist of thin upward growths of the posterior corners of the labial sclerite. The suture separating this portion of the labial sclerite from the occiput is called here the *paralabial suture*. Internally the dorsal portion of the postoccipital suture is represented by a strong ridge, while the lateral portions can be detected only as areas of heavy sclerotization. The labial suture is, however, represented by a rather strong ridge, at least in the ventral two thirds of its length.



FIGS. 6-7. *Danaus plexippus*. 6. Lateral view of head. 7. Antenna.

Lateral to the labial and postoccipital sutures, and covering the greater portion of the caudal surface of the head capsule, is the *occiput*. Approximately the inner one third of the occiput on each side of the foramen is separated from the remainder by two arcuate, heavily sclerotized streaks, the *transoccipital bands*.

In the center of the dorsal surface of the head is the *vertex*, an area delimited by the *transfrontal suture* anteriorly, the antennal sockets anterolaterally, and the *temporal suture* laterally and caudally. The temporal suture is represented internally by a rather

strong ridge, but both the suture and the ridge are indistinct near the antennal sockets and in the center of the caudal portion. Lateral to the temporal suture, and running parallel to it from the antennal sockets to the postoccipital suture, is the *paratemporal suture*, represented internally by a ridge which is not as distinct as that of the temporal suture. On the dorsal surface of the head the area between the two sutures is here called the *temporal area*; on the caudal surface of the head there is a U-shaped depression between the temporal suture and the paratemporal and postoccipital sutures, called here the *temporal fossa*. Within the fossa are two reniform areas (outlined with dotted lines in figure 4) in which there are a great many setae. These areas, possibly sensory, may be the chaetosemata of Jordan (1923).

It should be noted here that the homologies of the various features of the dorsal and caudal surfaces of the head capsule are much confused by the presence of secondary sclerotizations. The above interpretation has been necessarily arbitrary, in an attempt to arrive at names which can be employed throughout the comparative work which will follow this paper.

The *tentorium* consists of the posterior tentorial bar already described and two simple *anterior arms* running between the anterior and posterior tentorial pits. The anterior arms are somewhat thicker anteriorly than posteriorly. Between the anterior arms in the front of the head and attached to the cranial wall near the lower edge of the labrum is the sclerotic ventral part of the sucking pump. The structure is roughly semicircular and is made up principally of the *hypopharynx* (see Schmitt, 1938). The dorsal portion of the pump is not sclerotized and does not concern us here.

The compound eyes are separated from the head capsule by thin *ocular diaphragms*. These are membranous disks perforated by large oval openings (long axis dorsoventral) through which pass the optic nerves. The diaphragms each have a small sclerotized area bordering the opening.

THORAX

(Figures 8-21)

Prothorax: The prothorax is much smaller than either of the segments of the pterothorax. The *pronotum* is considered to be divided into three parts, a curved roughly triangular *dorsal plate*, and two flat, dorsomedially fused *lateral plates*. The dorsal plate is pointed at its posterior end, the beaklike point being curved ventrally

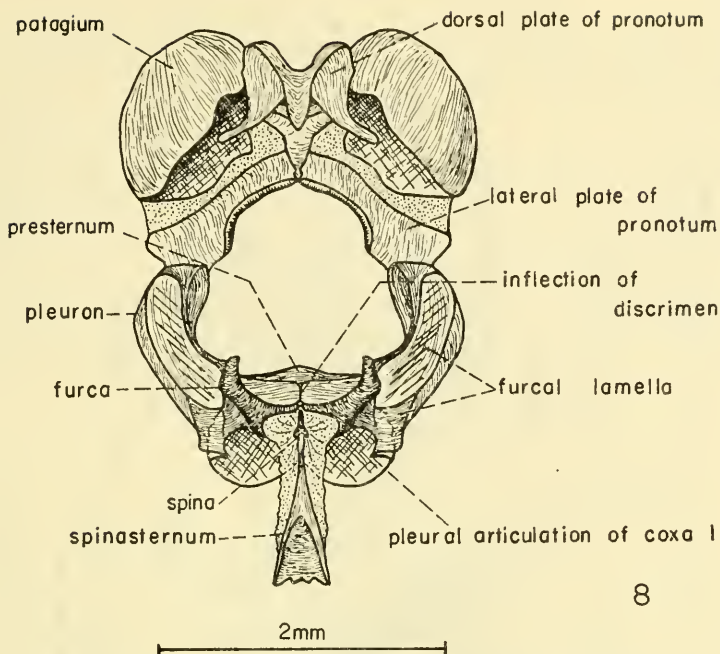


FIG. 8. *Danaus plexippus*. Posterior (internal) view of prothorax.

and articulated with the prescutum of the mesothorax. The fused portions of the lateral plates form a Y-shaped structure which articulates with the dorsal plate at the tips of the arms of the Y; the crotch of the Y is membranous. Just above the lateral plates of the pronotum and forward of the cephalic margin of the dorsal plate are the large, roughly hemispherical *patagia*. These well-sclerotized paired structures are the most conspicuous features of the dorsum of the prothorax. The ventral ends of the lateral plates of the pronotum are fused to the dorsal ends of the *propleura*, which in turn are fused with one another mid-ventrally, the fusion being indicated by a faint *discrimen*. Between the ring formed by the lateral plates of the pronotum and the propleura and the foramen magnum of the head is the membranous *cervix*. Bridging this cervical membrane lateroventrally on each side are the *cervical sclerites*. They are T-shaped, and each has a circular sclerotic pad bearing numerous setae on the stem of the T; the pads are called here *cervical organs*. The stem of the T articulates internally with the lateral extremity of the tentorial bridge and the upper arm of

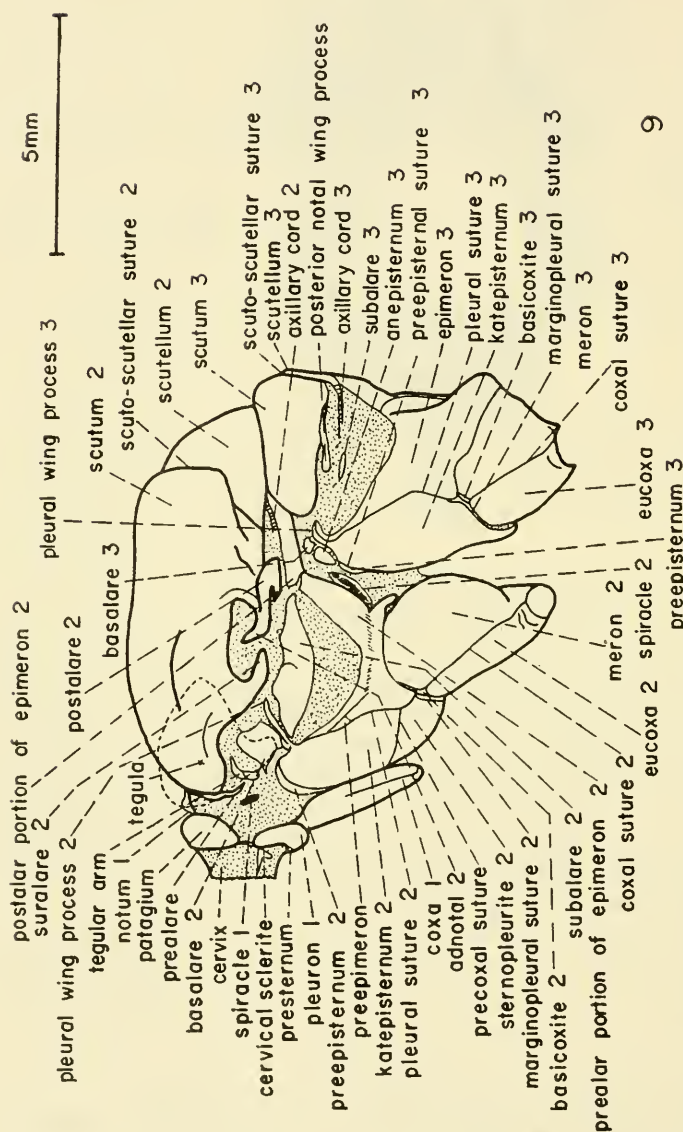


FIG. 9. *Danaus plexippus*. Lateral view of thorax. Broken line represents outline of tegula, removed to show structures beneath it.

the T externally with the dorsal part of the cephalic margin of the propleuron. Just forward of the line of fusion of the propleura, but not cut by the discrimen, is a narrow mid-ventral sclerite projecting into the cervix, called the *presternum*.

Internally the discrimen is represented anteriorly by a very weak inflection and caudally by a small *intercoxal lamella*. Laterocaudally on the rim of the coxal socket is the pointed *pleural articulation* of the coxa. Externally the discrimen may be traced between the bases of the coxae as a mid-line marking the base of the intercoxal lamella; it ends at the caudal margin of the coxal sockets at the oval *furcasternum*. In the center of the furcasternum can be

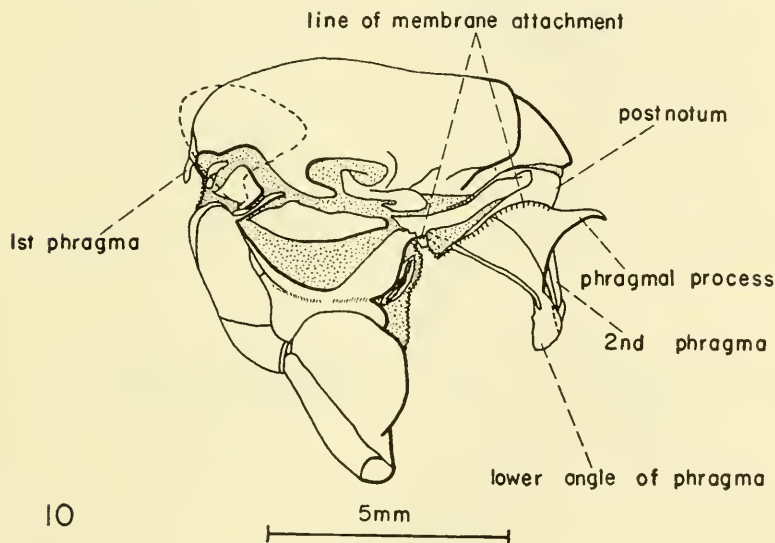


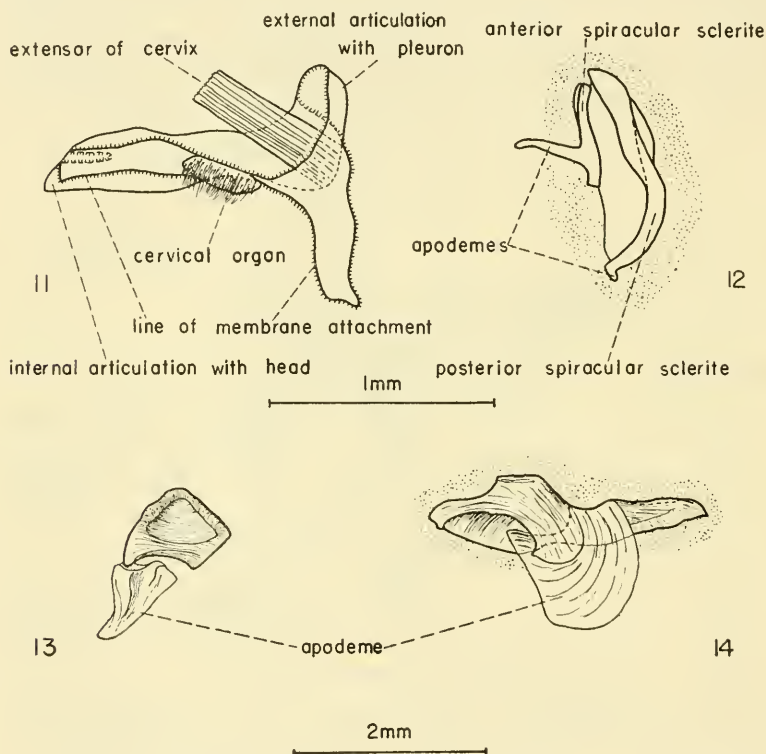
FIG. 10. *Danaus plexippus*. Lateral view of mesothorax, showing phragmata.

seen a dark area representing the *furcal pit*. Internally the furcasternum is produced into a heavily sclerotized two-pronged *furca*, which is joined to the pleuron by a plate which is to a large extent transparent, the *furcal lamella*.

Bridging the pro-mesothoracic intersegmental membrane mid-ventrally is a narrow sclerite, the prothoracic *spinasternum*. The spinasternum tapers to a point anteriorly where it joins the furcasternum of the prothorax, and gradually widens posteriorly, so that where it meets the mesothoracic katepisternum it is nearly as wide as the furcasternum. The caudal end of the spinasternum is notched

so that it joins the katepisternum at two points with a membranous triangle between them. Near its middle the spinasternum is deeply invaginated along with the adjacent membrane, forming an internal projection, the *spina*.

Mid-laterally in the pro-mesothoracic intersegmental membrane is the first *spiracle*. The upper half of the anterior border of the spiracular opening is occupied by the narrow *anterior spiracular*



FIGS. 11-14. *Danaus plexippus*. 11. Lateral view of cervical sclerite. 12. Mesal view of first thoracic spiracle. 13. Mesal view of mesothoracic basalare. 14. Mesal view of mesothoracic subalare.

sclerite, which bears near its ventral end a long apodeme. The entire posterior border of the opening is made up of the bandlike *posterior spiracular sclerite*, which has a small apodeme at its lower end.

Mesothorax: The *mesonotum* occupies the greater part of the dorsum of the pterothorax. It is divided into three sclerites, the *prescutum*, *scutum* and *scutellum*. The smallest of these, and the

most anterior; is the prescutum. It is curved strongly ventrally in front where it articulates with the pronotum, and bears on its anteroventral margin the thin bilobed *first phragma*. Arising from the lateral margins of the first phragma and hanging free in the body cavity are a pair of *phragmal arms*. Each lower lateral angle of the prescutum is produced into a long, slender process or *prealare*

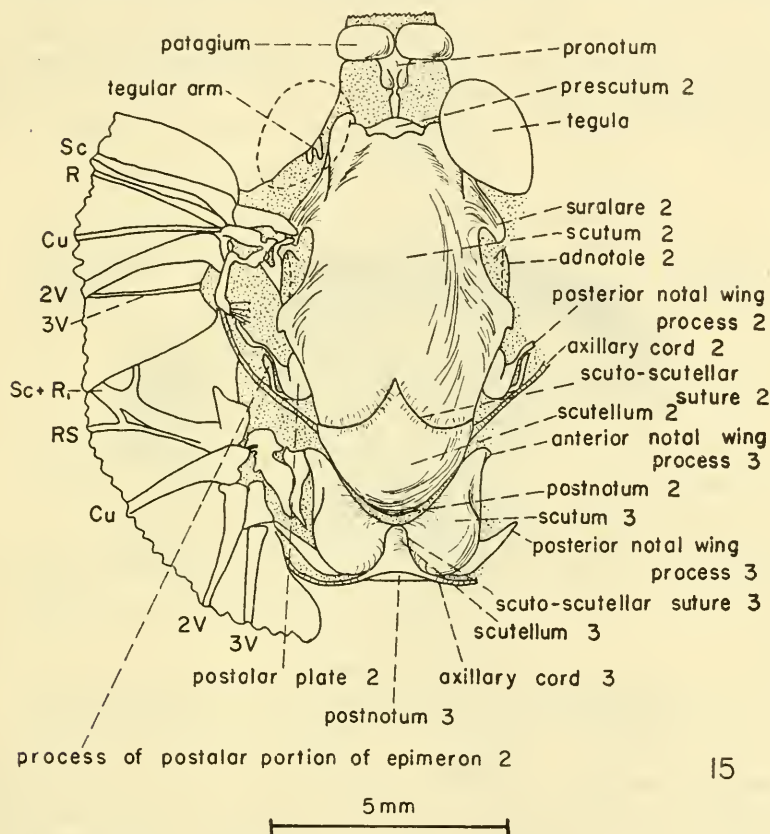


FIG. 15. *Danaus plexippus*. Dorsal view of thorax. Broken line represents outline of left tegula, removed to show structures beneath it.

extending latero-caudoventrally to just in front of the tegular arm. The suture between the prescutum and scutum is represented internally by a weak ridge.

The *mesoscutum* is the largest sclerite of the thorax. The lateral edges of the anterior part of the scutum are produced into sloping plates, the *suralares*. Internally each suralare is separated from the

main part of the scutum by a strong ridge, the *scutal ridge*, which runs from the posterior margin of the prescutum to the posterior margin of the scutal incision. The *scutal incision* is a deep notch in the lateral edge of the scutum just behind the suralare. From the scutum just behind the incision a plate, the *adnotale*, projects forward forming a lateral border for the posterior part of the incision. The first axillary sclerite articulates with both the suralare and the adnotale, which together make up the *anterior notal wing process*. Separating the scutum from the smaller *mesoscutellum* is the inverted V-shaped *scuto-scutellar suture*. This suture is represented internally by a strong ridge. Projecting forward and

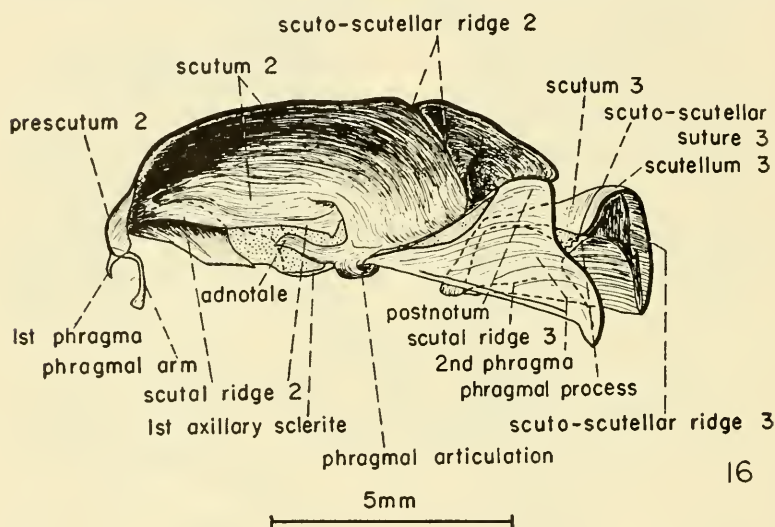


FIG. 16. *Danaus plexippus*. Mesal (internal) view of right half of meso- and metathoracic terga. Metapostnotum and third phragma omitted.

laterally from the end of the scuto-scutellar suture is a horizontal shelf, the *postalar plate*, the posterior portion of which is membranous. The anterior mesal part of the plate is in the form of a sclerotic arch which is continuous with the caudal part of the adnotale (this arch is hidden by the scutum in figure 28). The anterolateral corner of the postalar plate is produced as the *posterior notal wing process*, to which is fused the fourth axillary sclerite. Behind the membranous part of the plate is a thin sclerotic strip, and mesal to this strip is the base of the membranous axillary cord. Lateral to the plate and mesal to the axillary cord a rounded process

of the postalar portion of the epimeron projects through the membrane. This process is partially fused to the sclerotic part of the postalar plate.

A narrow membranous area separates the *postnotum* (the phragma-bearing plate) from the mesoscutellum. The *second phragma* is very large and somewhat triangular in lateral view, with dorsal

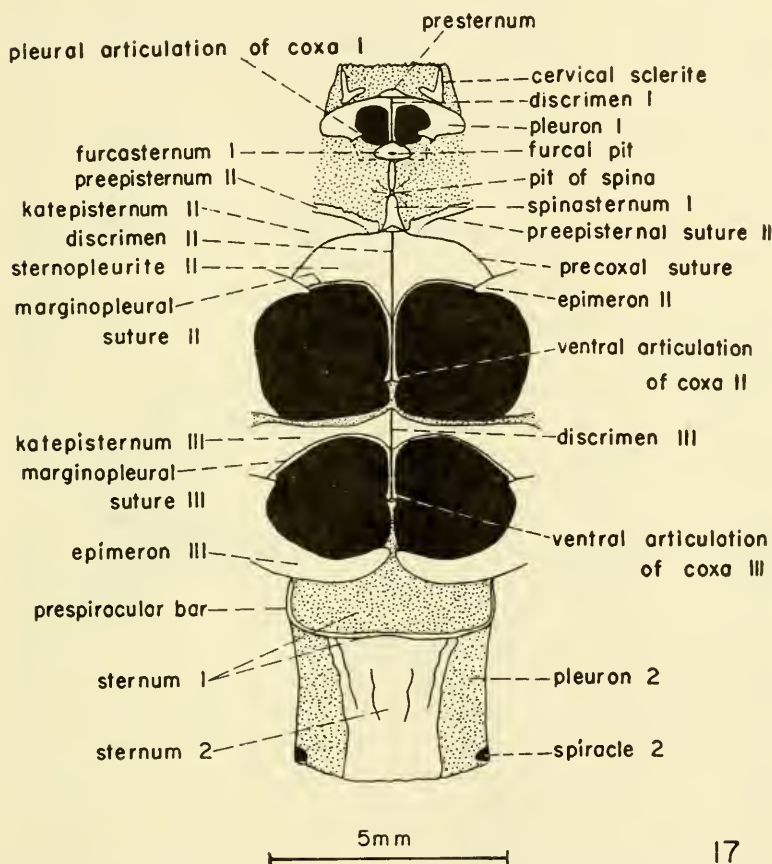


FIG. 17. *Danaus plexippus*. Ventral view of thorax and base of abdomen.

and ventral angles posteriorly and a mid-lateral angle forward. The anterior angles are paired, and each articulates with the mesoscutum in the socket of a protuberance of the ventral edge of the scutum immediately behind the caudal end of the adnotale, the *phragmal articulation*. Dorsally, at the rear of the phragma, are two prominent triangular projections, the *phragmal processes*, whose tips serve

for muscle attachment. The surface of the phragma itself displays a fairly complex pattern of ridges and varying sclerotization. Some major features of this pattern are a lightly sclerotized, anteriorly recurved area at the lower angle of the phragma, a heavily sclerotized bracing strut along the lower edge (sloping from the articulation almost to the lower angle), and two well-sclerotized ridges running ventrally from the lower bases of the phragmal processes to the lower angle. When viewed from behind, the lower angle of the phragma is not pointed but is fairly broad and bilobed. Continuous with the top of the phragmal process on each side, and arching cephaloventrally from it, is a ridge which joins the marginal strut and with it forms a small lateroventral protuberance. On this ridge is attached the meso-metathoracic intersegmental membrane. This line of membrane attachment separates the internal phragma from the external postnotum.

The more prominent features of the sternopleural region of the mesothorax are the *episternum*, *epimeron* and *coxa*. The *mesepisternum* consists of a large *katepisternum* with a tiny *anepisternum* nestled between the dorsocaudal corner of the katepisternum and the ventral side of the basalare. Approximately the lower third of the katepisternum is separated from the rest of the sclerite by the *precoxal suture*, which runs from the pleural suture to the anterior margin of the katepisternum at the point where it is joined by the prothoracic spinasternum. This part of the katepisternum is called here the *sternopleurite*. Immediately in front of the coxa the sternopleurite is traversed by the *marginopleural suture*, which runs from the pleural suture to the discrimen. The internal *marginopleural ridge* is strongest where it merges with the pleural ridge, becoming progressively weaker until it meets the base of the lamella of the discrimen. Internally the precoxal suture forms a strong ridge, the *precoxal ridge*, which is continuous with the thickened upper edge of the lamella of the discrimen. Above the precoxal suture the katepisternum is separated by a vertical suture, the *pre-episternal suture*, from a narrow anterior sclerite, the *pre-episternum*.

The pre-episternal suture is represented internally by the *pre-episternal ridge*. This ridge is rather small at its origin near the anterior part of the precoxal ridge, but becomes increasingly prominent as it curves dorsally and merges with the pleural ridge.

Mid-ventrally the sternopleurites unite in a suture, the *discrimen*, whose inflection forms the very high transparent *lamella of the discrimen*. The base of this lamella, in the form of two narrow strips

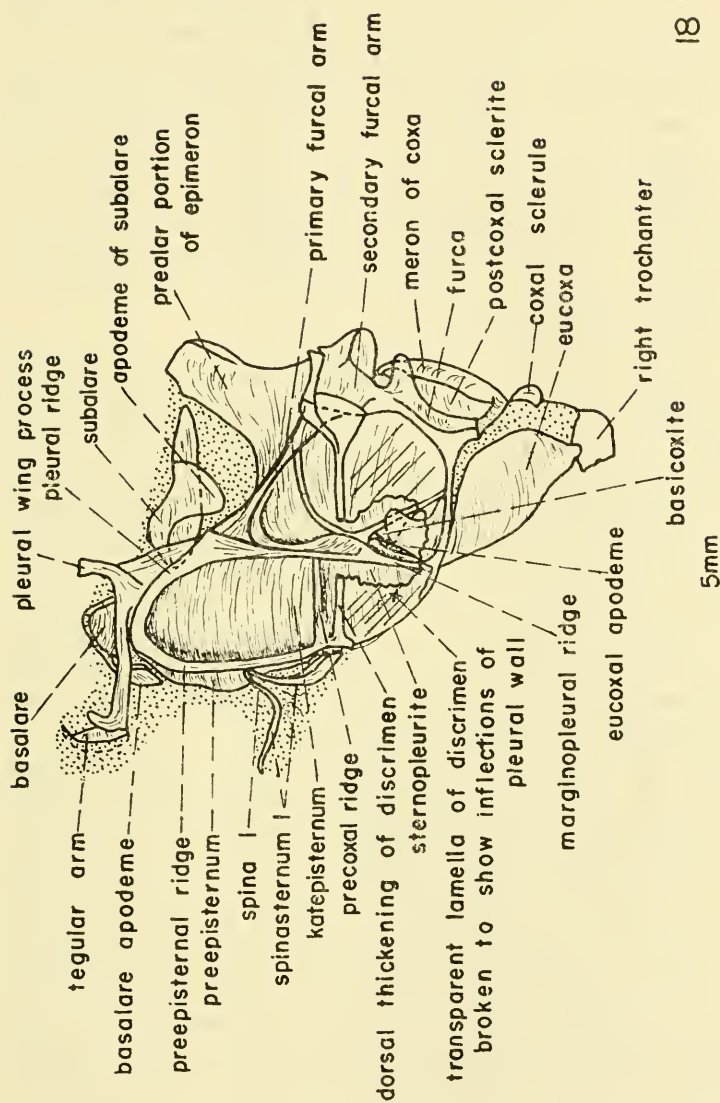


FIG. 18. *Danaus plexippus*. Mesal (internal) view of right half of mesopleuron and sternum and prothoracic spinasternum. Postalar portion of epimeron omitted.

of the sternopleurites, extends backward between the bases of the coxae to the *ventral articulations of the coxae*. Posteriorly the lamella of the discrimen merges into the mesothoracic *furca*, which arises from the discrimen above the coxal articulations. The furca, when viewed in caudal aspect, is roughly Y-shaped, the arms of the Y (the *secondary furcal arms*) fusing with the ventrocaudal corners of the prealar portions of the epimera. Running from the pleural ridges to the anteromesal parts of the secondary arms are the tendonlike *primary furcal arms*. The furca is a complex structure exhibiting varying degrees of sclerotization in different areas. Major features are three thin rounded lamellae projecting posteriorly from the main stem of the furca and from near the lateral borders of each of the secondary arms.

The mesepimeron is divided into two parts, an anterior *prealar portion* and a posterior *postalar portion*. The dorsal edge of the prealar portion curves strongly downward near the middle, leaving a relatively large area between it and the ventral side of the subalare. Near the dorsal part of the anterior border of the epimeron a small plate is separated from it, the *pre-epimeron*. The postalar portion is separated from the dorsocaudal corner of the prealar section by a line. The anterior end of this portion is inflected and curved downward into the body cavity as an apodeme and upward as a process which penetrates the two membranes mesal to the axillary cord and emerges lateral to the postalar plate. Externally the postalar portion of the epimeron appears as a long strip which fuses caudally with the dorsal part of the postnotum.

Between the epimeron and the episternum is the deeply inflected *pleural suture*. The internal manifestation of this suture, the *pleural ridge*, is the most prominent feature of the mesal wall of the mesothorax. Near its dorsal limit, at the point of attachment of the primary furcal arms, the ridge is produced mesocaudally into a small plate. The inflection producing this plate is responsible for the formation of the pre-epimeron, although the deep inflection of the pleural suture in this area makes the exact method of its formation difficult to determine. Narrow strips of the anepisternum and epimeron, carrying with them the pleural suture, project dorsally between the basalare and subalare as the *pleural wing process*. From this process just mesal to the caudoventral corner of the basalare a tubular internal process projects anteriorly behind the basalare, the *tegular arm*. The arm terminates just in front of the basalare in two lobes, one mesal to the other, whose surfaces are

external. Articulating with the lateral lobe of the arm is the large bilobed *tegula*. The smaller lower lobe of the tegula curves beneath the leading edge of the wing.

In the region of the pleural coxal articulation the pleural ridge becomes a quite complex structure as it is joined by the precoxal ridge, the marginopleural ridge, and the ridges formed by the inflected dorsal and anterior margins of the meron. The *coxa* (which is discussed here because it is an integral part of the thoracic capsule) consists of two sclerites, a relatively narrow anterior *eucoxa* (Madden, 1944, not Michener) and a bulbous posterior *meron*. The suture between the two (the *coxal suture*) seems to be a line suture, with the internal ridge representing the inflection of the border of the meron alone. The dorsomesal border of the eucoxa is inflected and produced into the relatively large *eucoxal apodeme*. The caudo-ventromesal part of the coxa is membranous, containing one round sclerotic island, the *coxal sclerule*. A small caudomesal lip of the upper part of the meron, the *postcoxal sclerite*, is separated from the rest of that structure by the *postcoxal suture*, which is represented internally by a weak ridge continuous with the inflected border of the meron. At the top of the coxal suture there is a tiny sclerite, a lip of the meron beyond its inflected edge, the *basicoxite*.

Above the episternum in front of the pleural wing process is a roughly diamond-shaped plate, the *basalare*. Internally a triangular cavity occupies the central part of the sclerite. A large, for the most part lightly sclerotized apodeme is attached by an almost transparent tendon to the anterior corner of the basalare. Above the epimeron, and separated from it by a considerable expanse of membrane, is the other epipleurite, the large elongate *subalare*. Internally the subalare has a concavity anteroventrally, and bears a conspicuous winglike apodeme projecting from its mid-section into the body cavity.

In the meso-metathoracic intersegmental membrane close to the upper part of the prealar portion of the epimeron, is the second *spiracle*. It is bordered in front and behind by fringed, lightly sclerotized plates, the *anterior* and *posterior spiracular sclerites*.

Metathorax: In the *metanotum* the *metascutum* is divided into two lateral portions by the *metascutellum*. The *scutoscutellar ridge* is very strong and wall-like, dividing the bulging upper part of the metanotum into three compartments. The *anterior notal wing processes* are merely small projections of the anterolateral

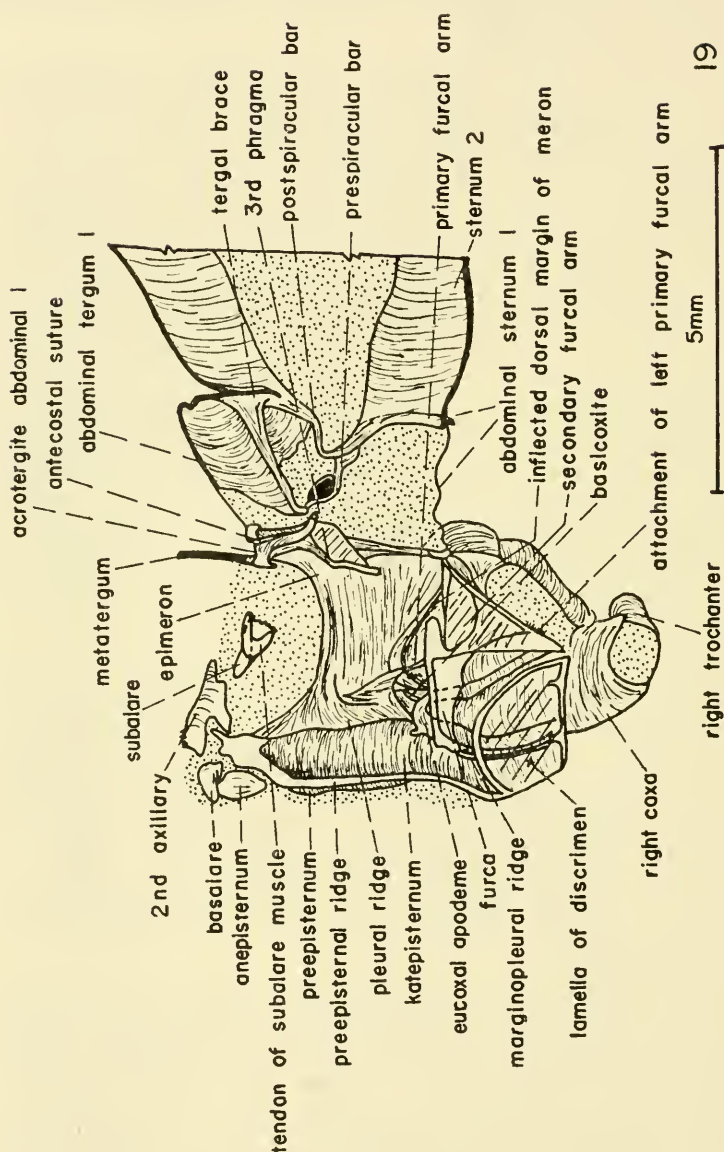
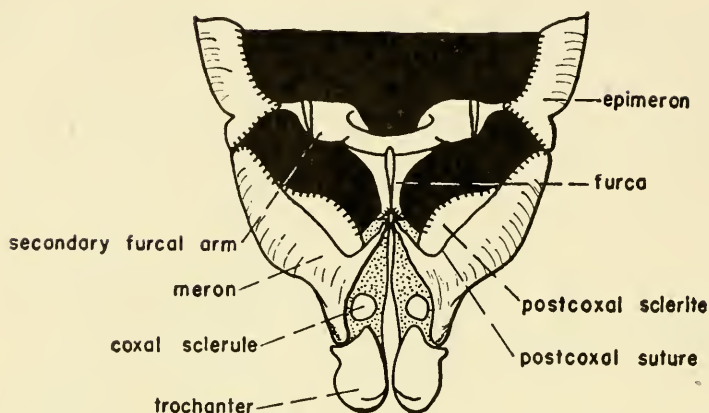


FIG. 19. *Danaus plexippus*. Mesal (internal) view of right half of metapleuron and sternum and base of abdomen.

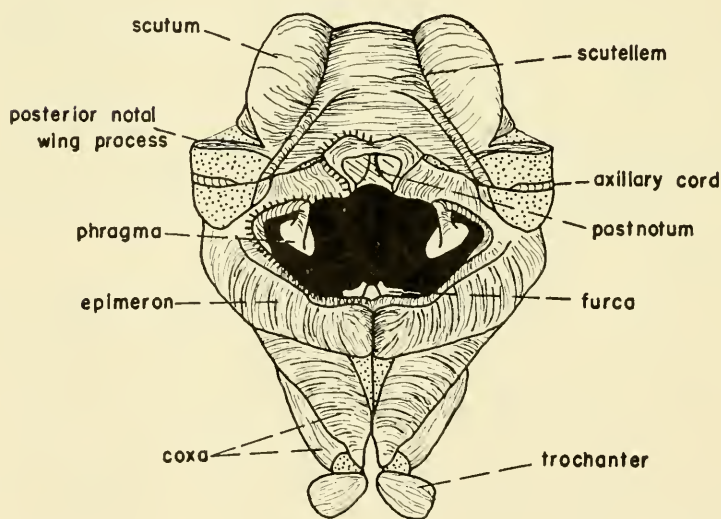
walls of the scutum, while the *posterior notal wing processes* are long slender projections from the posterior part of the scutum. The *scutal ridge* is present in the same position as in the mesoscutum, but is, of course, much shorter. There is no scutal incision. A thin membranous area separates the complex *metapostnotum* dorsally from the metascutellum. The salient features of the postnotum are a ventrally truncated heart-shaped area at the mid-line of the dorsum, and the phragma which is divided into two arms, each tipped with a flat oval plate, which project into the body cavity from near the lateral extremities of the postnotum. The whole postnotum is so well fused with the tergum and epimeron laterally that its limits are difficult to ascertain.

As can be seen from the figures, the positions of the various sclerites of the metathoracic pleural and sternal areas are very similar to the positions of the homologous sclerites of the mesothorax, although their shapes are quite different. Therefore only major differences will be discussed here. The *anepisternum* is a small but well-defined sclerite just above the shoulder of the *katapisternum*. It bears numerous bristles, and although it is closely associated with the basalare and pleural wing process it is separated from each by a distinct line suture. The precoxal suture is absent, leaving the katapisternum as an undivided sclerite. There is an insignificant *pre-episternum*, which does not continue ventrally to the level of the coxa. The *meron* is sharply reduced in favor of the *epimeron*.

Internally the metathorax presents quite a different aspect from the mesothorax. The *lamella of the discrimen* is arched, arising at the base of the *pre-episternal ridge* and terminating at the base of the *furca*. The top of the lamella is thickened as in the mesothorax, and there are two short pointed thickenings in the base of the lamella. There is, of course, no precoxal ridge. The *eucoxal apodeme* has on its dorsum a small tubercle to which a muscle is attached. The *metafurca* is entirely different from the mesofurca. Its most prominent feature is a forward-thrust structure, shaped somewhat like an arrowhead when seen in dorsal aspect, which overhangs the lamella of the discrimen. The posteriorly projecting *secondary arms* are fused together ventrally forming a V-shaped trough which becomes progressively shallower caudally. The arms are thin and are broadly fused to the epimera which are curved mesally and form the caudal border of the thorax beneath the attachment of the abdomen. The



20



5mm

21

FIGS. 20-21. *Danaus plexippus*. 20. Posterior view of mesothorax, tergum omitted (the line marked by short cross lines represents attachment of meso-metathoracic intersegmental membrane). 21. Posterior view of metathorax (line of metathorax-abdominal intersegmental membrane indicated on left half of figure only).

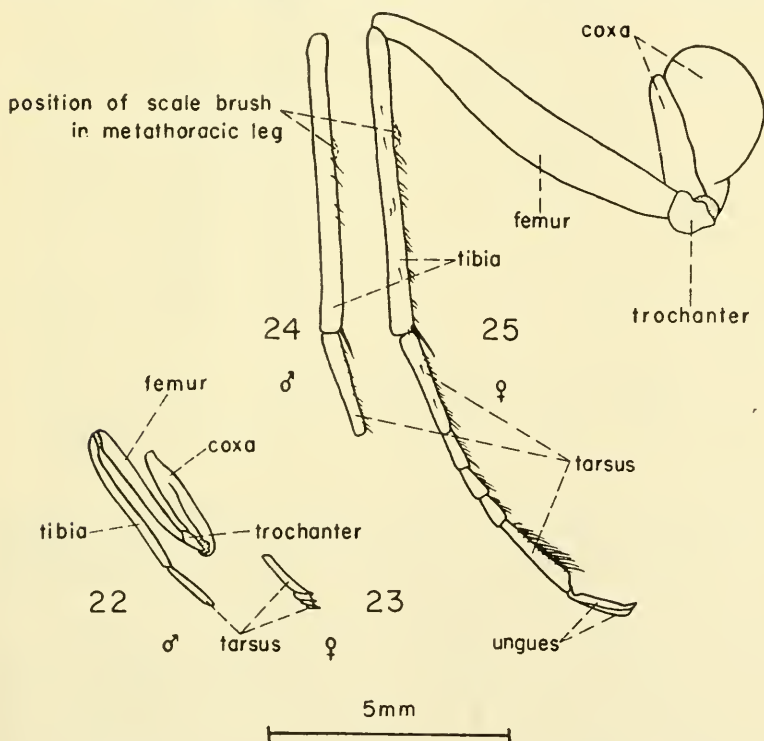
transparent, tendonlike *primary furcal arms* arise near the base of the furca and attach to a plate which seems to be an outgrowth of both the pleural ridge and the epimeron just posterior to it. There is, however, no obvious pre-epimeron. The tegular arm and tegula are absent.

The *basalare* is much smaller than that of the mesothorax, and bears on its inner surface a relatively large blunt *basalare apodeme*. The *subalare* is small and seems to be merely an external manifestation of a sclerotic cap to which the subalare muscle is attached.

LEGS

(Figures 22-27)

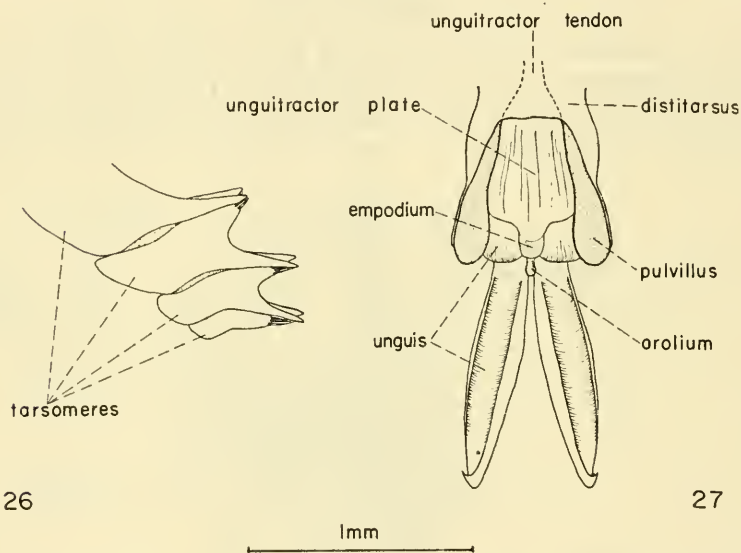
The prothoracic legs of *Danaus*, as in all other so-called "four-footed butterflies," are greatly reduced. The *procoxa* is long (approximately the same length as the *profemur*) and grooved on its lateral face. The male *tarsus* is simple (not divided into tarsomeres)



FIGS. 22-25. *Danaus plexippus*. 22. Prothoracic leg of male. 23. Protarsus of female. 24. Tibia and basal tarsomere of mesothoracic leg of male. 25. Mesothoracic leg of female.

while that of the female is club-shaped and divided into four *tarsómeres*, a long proximal one, and three compressed distal ones. On the caudal side of the distal end of the first three tarsómeres are paired spines. These are complemented by lobes on the caudal side of the proximal end of the last three tarsómeres which bear bundles of setae which cup around the bases of the spines.

The meso- and metathoracic legs are similar in both sexes. In specimens which have the scales intact, however, there is a small brush of narrow setalike scales somewhat more than halfway up the mesal side of the tibia of the mesothoracic leg. This is absent



FIGS. 26-27. *Danaus plexippus*. 26. Detail of distitarsus of prothoracic leg of female. 27. Ventral view of pretarsus of pterothoracic leg.

in the metathoracic leg. The tibiae of the mesothoracic and metathoracic legs in the females bear numerous spines, while there are only a few scattered spines in the males. The spines of the proximal tarsomere are also more prominent in the female.

In the *pretarsus*, the *unguifer* (the dorsal plate to which the *tarsal claws* or *ungues* are articulated) is only slightly sclerotized. The most prominent feature of the ventral side of the pretarsus is the large flat *unguigractor plate*. This plate is tapered internally into a long thin apodeme, the *unguigractor tendon*. Just in front of the unguigractor plate, between the basal parts of the claws, is a small,

membranous lobe, the *empodium*. Just dorsal to the empodium is a small lightly sclerotized protuberance, the *arolium*. Lateral to the unguitractor plate are two membranous lobes, the *pulvilli*. The ungues are not notched, and are abruptly hooked terminally and thickened basally.

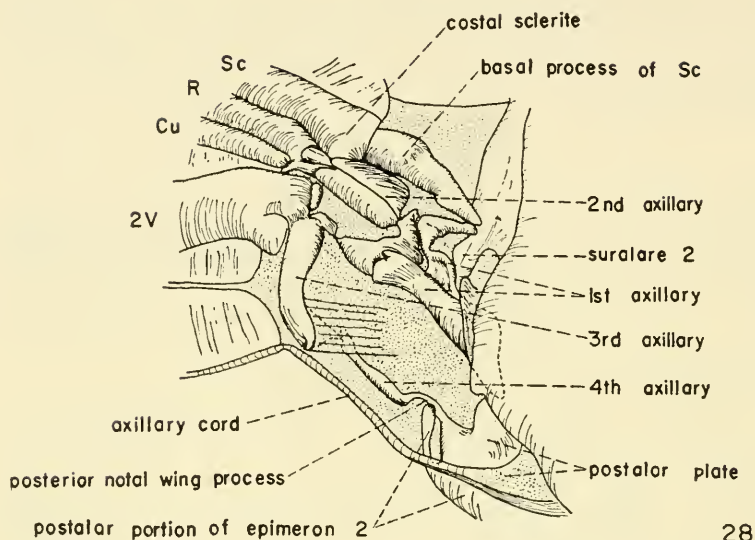
WINGS AND WING BASES

(Figures 28-31, 33)

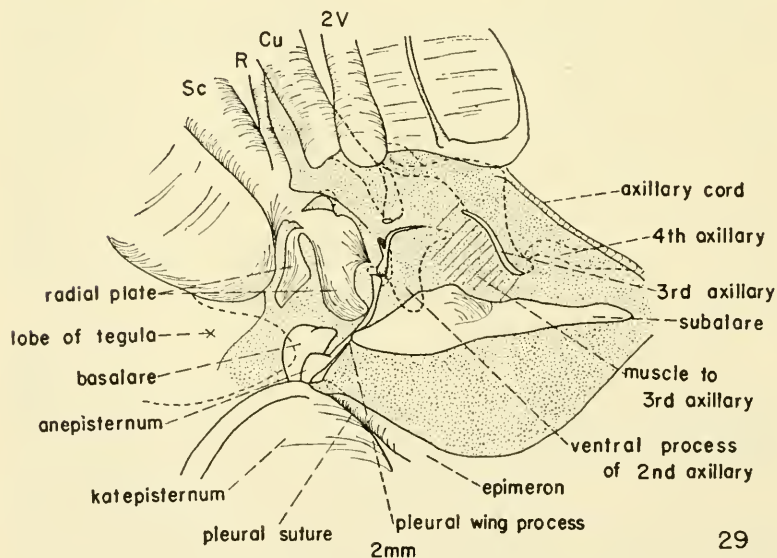
The areas of the wing articulations present an extremely complex picture. Each area consists of two membranes and associated sclerotic plates; an upper membrane connecting the dorsum of the wing with the tergum, and a lower membrane connecting the venter of the wing with the pleurites. These membranes are called the *upper* and *lower alary membranes* respectively.

In these membranes are found a series of plates which are among the most important structures of the wing articulation, the *axillary sclerites*. In the mesothorax there are four axillary sclerites. The *first axillary* is visible only from the upper side. It is roughly Y-shaped, with the base of the Y articulating with the adnotale, the anterior arm with the suralare mesally and the second axillary laterally, and the posterior arm with the second axillary. The *second axillary* is bilobed when viewed from above. The mesal lobe articulates with the first axillary mesally and the third axillary posterolaterally; the lateral lobe is narrowly fused to its anterolateral corner. Distally the lateral lobe is in contact with the complex basal sclerotizations of veins Sc, R, Cu and 2V. Beneath the upper alary membrane both lobes of the second axillary send plates ventrally which fuse into a blunt process. This process articulates with the pleural wing process, a small portion being exposed ventrally.

The *third axillary* is V-shaped, with the distal arm of the V lying in the upper membrane and appearing from above as a slightly arcuate oblong sclerite. The proximal arm projects ventromesally between the membranes from the caudal end of the distal arm. A small portion of it penetrates the lower membrane and can be seen as a narrow strip above the subalare. The muscle of the third axillary sclerite is attached to the crotch and proximal arm of the V. The *fourth axillary* lies in the upper membrane and is fused to the posterior notal wing process, from which it is differentiated by a constricted area. Its distal end lies under the flap of membrane enclosing the third axillary muscle and works against the proximal arm of the third axillary.

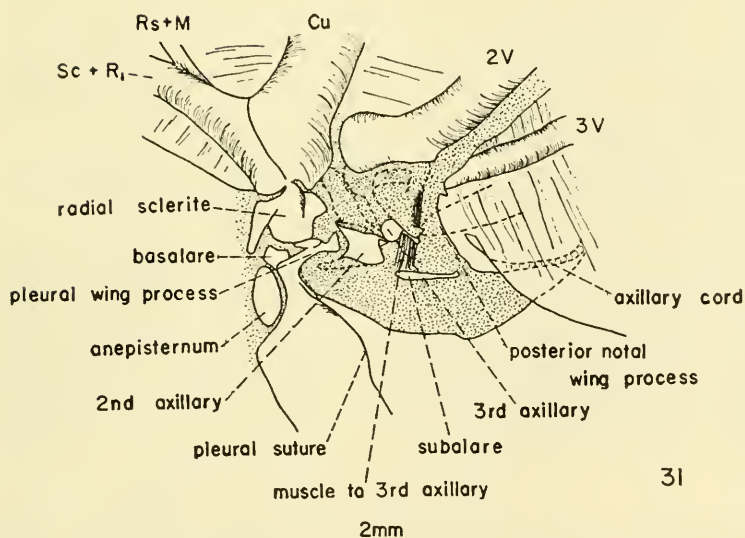
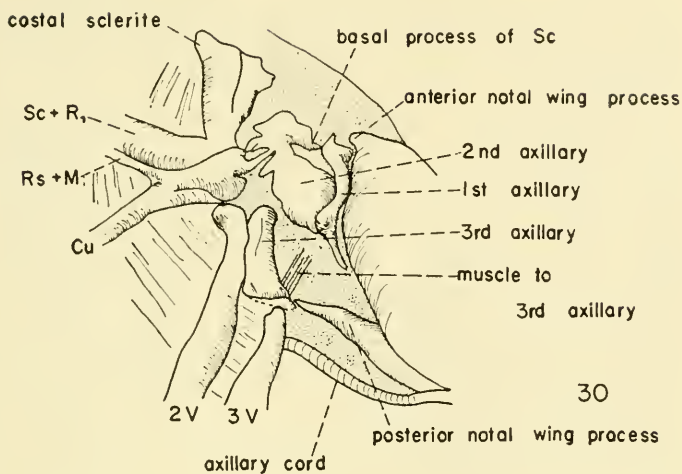


28



29

FIGS. 28-29. *Danaus plexippus*. 28. Dorsal view of mesothoracic wing base, wing held horizontal. 29. Lateral view of mesothoracic wing base, wing held vertical.



FIGS. 30-31. *Danaus plexippus*. 30. Dorsal view of metathoracic wing base, wing held horizontal. 31. Lateral view of metathoracic wing base, wing held vertical.

In front of the first and second axillary sclerites is the pointed *basal process of the subcosta* (Sc), which articulates with the suralare and the anterior arm of the first axillary. On the ventral side the base of the fused Sc + R is expanded into a bilobed sclerite, the *radial plate*.

In the metathorax there are only three axillaries, the fourth axillary being absent. The pattern of the sclerites is similar to that of the mesothorax, although their shapes are quite different. The *first axillary* is long and thin, with the posterior arm of the Y reduced to a mere bulge. The *second axillary* is very irregular and is fused anteriorly with the *basal process of the Sc*. Near the lateral edge, the second axillary bears a ventral process which penetrates the lower alary membrane, producing a rather large, ventrally exposed sclerite which articulates with the pleural wing process.

The *third axillary* is shorter than that of the mesothorax, and the muscle is smaller. It is more triangular than V-shaped. The portion visible from above is oblong, and the anterior and posterior ends of this portion are inflected ventrally and fused together to form a process which penetrates the lower membrane. The muscle is attached to the upper posterior angle of the rough triangle thus formed. The posterior notal wing process articulates with the caudomesal side of the lower apex of the triangle.

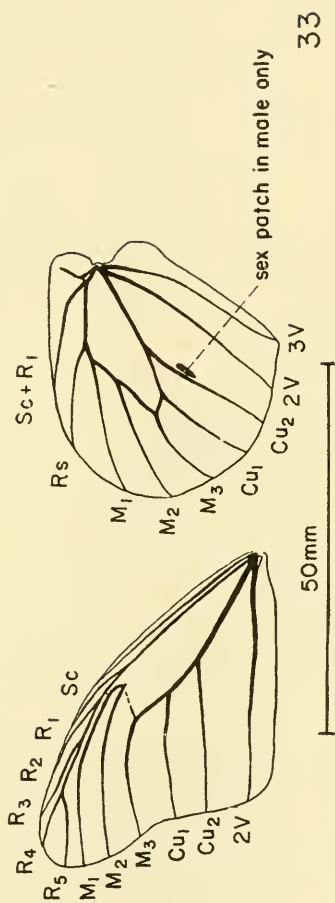
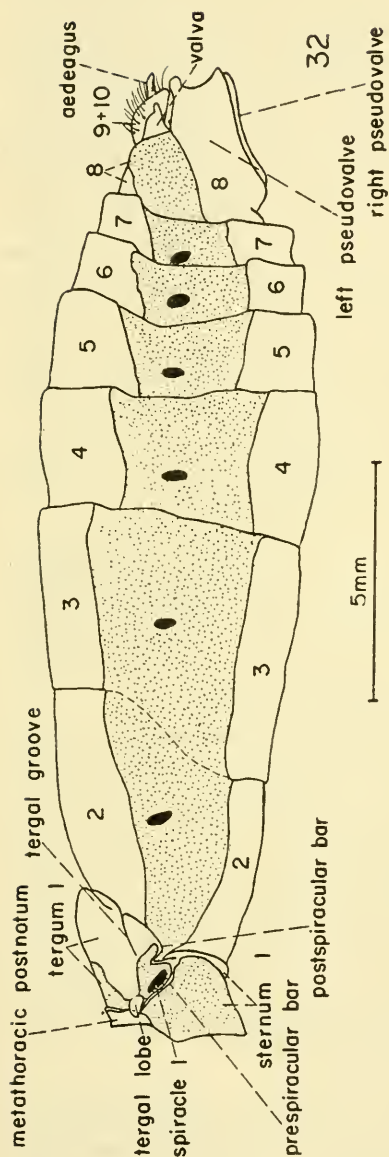
Just mesal to the base of Sc + R₁ and projecting anteriorly is a large *costal sclerite*. On the underside a bilobed *radial sclerite* is present.

Figures of the wing venation are presented for completeness and for orientation in connection with the figures of the wing bases. The venation of the monarch has been figured numerous times before, and nothing new is added here. The system of naming the veins is adopted from Klots (1951) with the substitution of *vannal veins* for "anal veins."

ABDOMEN

(Figures 32, 34-41)

Pregenital segments: Because of the modification of the eighth sternum of the male into pseudovalves, it can be said that there are seven pregenital abdominal segments in both sexes of *Danaus plexippus*. The first abdominal segment is highly modified, as in most higher insects, for articulation with the metathorax. The anterior part of *tergum 1* is membranous. The sclerotic portion of the tergum is dorsocaudally bulged, giving a pouchlike effect. Its



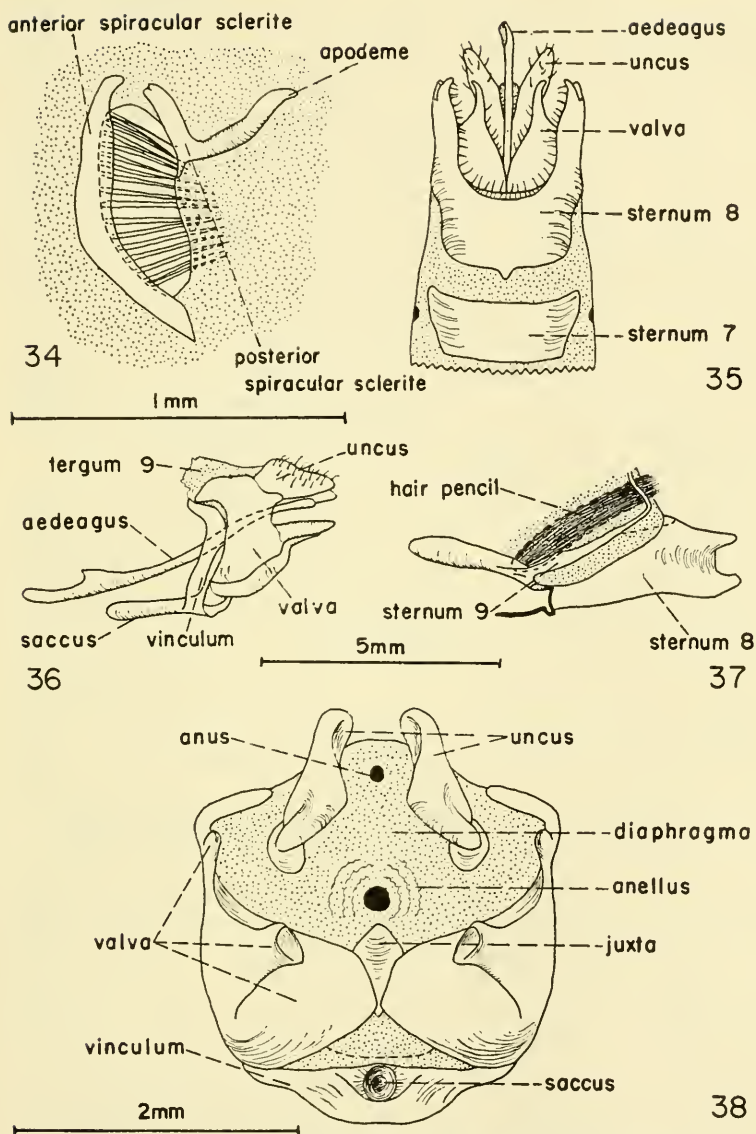
FIGS. 32-33. *Danaus plexippus*. 32. Lateral view of male abdomen. 33. Wing venation.

caudal margin slightly overhangs the second abdominal tergum. On each side of the first tergum, near its margins, is a deep inflection, the *tergal groove*. The heavy internal ridge of this inflection is called the *tergal brace*. The anterolateral corners of the tergum are produced laterally into small protuberances, the *tergal lobes*. The first abdominal sternum (*sternum 1*) is almost completely membranous, only a small posterior sclerotic portion remaining which is fused to *sternum 2*. This portion of the sternum is also fused to a thin process of the posterolateral corner of the tergum, the *postspiracular bar*. Just in front of this point of fusion another thin process is emitted by the sternum which crosses the pleural area below the first abdominal spiracle and terminates just below the tergal lobe (not fusing with it). This process is called the *prespiracular bar*. The abdominal spiracles are all similar to the first thoracic spiracle but the abdominal *anterior spiracular sclerites* resemble the thoracic posterior spiracular sclerites and vice versa. There are brushes of bristles extending externally and caudally from the anterior spiracular sclerites of the abdomen.

The first, second, and third *terga* and *sterna* are fused together and lack intersegmental membranes. From the 3-4 intersegmental area onward there is an increase in the amount of intersegmental membrane and the resultant amount of possible overlap of segments. The size and shape of pregenital segments 2-7 can be seen in figure 32. None of them bear significant internal processes.

Male genital segments: The eighth tergum is somewhat reduced. The eighth sternum is fairly normal, though lightly sclerotized, for the first one fourth of its length. Its caudal portion, however, is heavily sclerotized and inflected, forming a U-shaped structure below and around the genitalia proper. The extreme caudal portions of the sternum extend beyond the pleural membrane as hollow bilobed protuberances. These eighth sternal structures have the appearance of paired valvae, and are called here *pseudovalves*, following Viette (1948). It should be noted that Klots (1956) is in error in regarding Viette's term as applying to enlargements of the ninth sternum (probably a *lapsus calami*).

Between the eighth and ninth *sterna* there is on each side an invagination of the intersegmental membrane which contains a *hair pencil*. The ninth sternum is a narrow U-shaped sclerotic band, termed by taxonomists the *vinculum*. Mid-ventrally it bears a blind tubular apodeme directed anteriorly, the *saccus*. Articulated to the lateral arms of the vinculum are the paired *valvae*, morpho-

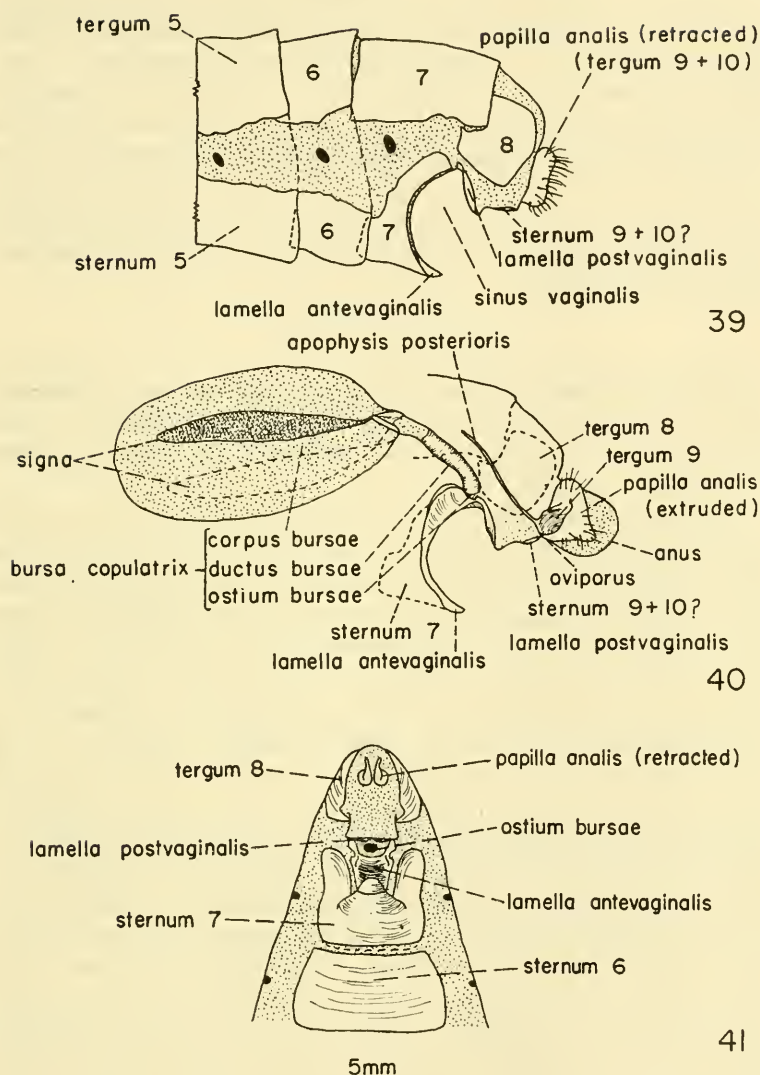


FIGS. 34-38. *Danaus plexippus*. 34. Mesal view of fourth abdominal spiracle. 35. Ventral view of apex of male abdomen. 36. Lateral view of male genitalia proper (setae of valvae omitted). 37. Mesal view of right pseudovalve (setae omitted), hair pencil and sternum 9. 38. Posterior view of male genitalia proper (setae omitted).

logically probably the gonocoxites of the ninth segment. Each valva bears a sharp elongate caudomesal process. The ninth tergum, which in most Lepidoptera makes up the major portion of the heavily sclerotized tegumen, is membranous. The region of the tenth tergum is occupied by two fairly lightly sclerotized lateral lobes, termed collectively the *uncus*. There is no sign of a gnathos, or any other sclerotization of the tenth sternum. A membrane closes the rear end of the abdominal cavity, running from the bases of the valvae and the vinculum to the uncus and anus. This terminal membrane is referred to as the *diaphragma*. The *anus* is situated in the lobe of the membrane which separates the parts of the uncus. The diaphragma is pierced roughly in its center by the long slender heavily sclerotized *aedeagus*. The eversible cone of membrane around the aedeagus is termed the *anellus*. The only sclerotization in the diaphragma proper is a roughly triangular *juxta* lying below the aedeagus and presumably helping to support it.

Female genital segments: Although it is not properly a genital segment, it should be mentioned that the seventh sternum is somewhat modified to extend up and around the anterior borders of the sinus vaginalis. The *sinus vaginalis* is a conspicuous cavity in the ventral side of the abdomen, just caudal to the seventh sternum. The sinus contains two sclerotic plates, a large anterior deeply incurved *lamella antevaginalis*, and a smaller posterior *lamella postvaginalis*. The two lamellae are joined laterally and enclose a small membranous area in the center of which is the receptive opening, the *ostium bursae*. Internally the heavily sclerotized *ductus bursae* leads from the ostium to the large membranous *corpus bursae*. In the wall of the corpus bursae is a pair of spined *signa*, joined by a yoke at the anterior end of the corpus. The corpus, ductus and ostium bursae together comprise the *bursa copulatrix*. The lamella antevaginalis is a structure of the 7-8 intersegmental membrane and can be differentiated from the seventh sternum, while the lamella postvaginalis, also presumably intersegmental in origin, cannot be distinguished from the eighth sternum. The eighth tergum is divided into two lateral plates, its dorsum being membranous.

The only well-sclerotized structures beyond the eighth segment are two lateral plates fused to the papillae anales, which bear the *apophyses posteriores*, strongly sclerotized paired apodemes which project forward into the body cavity. These plates are considered to represent the ninth tergum. The *papillae anales* are lightly



FIGS. 39-41. *Danaus plexippus*. 39. Lateral view of apex of female abdomen. 40. Lateral view of apex of female abdomen showing internal structures. 41. Ventral view of apex of female abdomen.

sclerotized setose lobes on either side of the membranous bulge of the anal area. They are presumably derived from the ninth or tenth terga or both. Just below and anterior to the papillae is a small lightly sclerotized area which may be a remnant of the ninth or tenth sterna or both. The *anus* and *oviporus*, the former above and behind the latter, lie between the papillae. The ninth and tenth segments can be retracted within the eighth so that only the tips of the papillae can be seen, or they may be completely extruded so that the bulging lightly ridged membrane around the anus protrudes between the papillae.

VARIATION

In the descriptive section of this work no mention is made of individual variation between the specimens examined. Disregarding sexual dimorphism two types of variation were observed: variation in size and variation in shape. However, the structures studied were invariably present.

Variation in size was not extreme. The length of a primary (mesothoracic) wing from the base of the subcosta to the apex has been studied in order to give an idea of the magnitude of this variation. Twenty-one male specimens from Lawrence, Douglas County, Kansas showed a range for this measurement of 48-55 mm., with a mean of $51.2 \pm .48$ mm. Fourteen females from the same locality showed a range of 49-57 mm., with a mean of $52.1 \pm .67$ mm.

Variation in shape was also relatively slight. Some of it can be attributed to the circumstances of the insect's death (whether it was pinched, placed in a cyanide jar, or placed directly in fixative); the outline of the thoracic terga or the amount of membrane exposed between the meso- and metathoraces or the katapisternum and eucoxa of the metathorax may be affected. Proportions of various structures may vary, such as the ratio of the length of the mesoscutellum to the mesoscutum. The courses of most of the sutures show variability, some (*e. g.*, the mesothoracic scuto-scutellar) being rather variable, while others (*e. g.*, the mesothoracic pleural) being relatively stable. Sclerites in which greater than average variation in shape has been observed are, among others, the epimera of the pterothorax, the mesothoracic subalare, and the mesoscutellum. However, it should be emphasized that this variation is still relatively minor and that in no case is the characteristic shape of the sclerite lost.

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[No. 19

A Revision of the Subgenus *Melanonemotelus* of America North of Mexico (Diptera, Stratiomyidae)*

BY

WILFORD J. HANSON

ABSTRACT. This is a revision, based primarily upon male genitalic characters, of the American species of *Melanonemotelus*, genus *Nemotelus*, north of Mexico. Previous to this paper 15 species from this region had been described. Nine new species are described, and all old species are redescribed. Five species are placed in synonymy. In addition, the range of the European species, *Nemotelus nigrinus* Fallén, is extended to this region, as four American species are placed in synonymy with it.

New species described: *Nemotelus politus*, *N. jamesi*, *N. variabilis*, *N. centralis*, *N. halophilus*, *N. sabroskyi*, *N. communis*, *N. picinus*, *N. tenuistylus*.

Species placed in synonymy: *Nemotelus carneus* Walker 1849 (syn. of *N. nigrinus* Fallén 1817), *N. crassus* Loew 1861 (syn. of *N. nigrinus* Fallén 1817), *N. unicolor* Loew 1861 (syn. of *N. nigrinus* Fallén 1817), *N. carbonarius* Loew 1865 (syn. of *N. nigrinus* Fallén 1817), *N. fulvicornis* James 1936 (syn. of *N. glaber* Loew 1872).

INTRODUCTION

The subgenus *Melanonemotelus* of the genus *Nemotelus* has long been in need of revision. These flies possess few distinct external characters which are useful in their determination. For this reason and because of great individual variation, there has been much taxonomic confusion. Examination of the male genitalia showed the extent of this confusion. It became apparent that several described species were poorly defined and that several were as yet undescribed. This revision of the subgenus *Melanonemotelus* is based primarily on male genitalic characters. These characters generally exhibit noticeable diversity between species which otherwise appear the same. They are, however, relatively stable within species and are thus considered reliable. Because of the simplified

* Contribution number 925 from the Department of Entomology of the University of Kansas.

structure of the female genitalia, no usable characters were found there. Thus as might be expected, the females of several species are very similar, and determination is often impossible without males.

The range of *Melanonemotelus* includes North, Central and South America, the West Indies, northern Europe, and presumably northern Asia. This revision includes only those species of North America north of Mexico. The type specimens of the three described species from Mexico have been destroyed, and because of the lack of sufficient material and absence of genitalic description or illustration of the types, further consideration of species from this region is not feasible at this time.

The occurrence of these flies is sporadic. At certain times they appear by the thousands on their favorite host flowers. The adults are sluggish and, while feeding, may be taken by hand. Umbellifers and composites such as goldenrod are among the preferred host flowers.

Little is known of the immature stages. The larvae of *Nemotelus* (s. str.) are known to be aquatic, some living in saline water. It seems likely that larvae of *Melanonemotelus* occur in similar habitats. *N. (Melanonemotelus) melanderi* and *sabroskyi* are limited to the Atlantic coast. *N. (Melanonemotelus) halophilus* has been collected only along the Texas gulf coast and from salt marshes in New Mexico and Kansas. The author has collected *N. (Melanonemotelus) nigrinus* along mountain streams in Utah.

The flies of this subgenus are very small in comparison with most other Stratiomyidae and are shining black, usually with yellowish markings. In two species from Florida and the West Indies the males differ from all others of the subgenus in having abdomens predominantly whitish. The face of *Melanonemotelus*, as in all *Nemotelus*, is produced anteriorly into a cone to accommodate the long proboscis. The male and female differ strikingly in the head. The males are holoptic, the eyes very large and covering most of the head. The frontal spots, when present, are contiguous. In the female the eyes are smaller, the frontal spots separated, and the facial prominence longer (Figs. 1-8). The wing venation is much reduced, the posterior veins merely impressions in the wing membrane.

An attempt was made to find some characters in the genitalic structure of each species which might indicate relationships. However, where it was possible to group species according to similarities

in genitalia, it was found that the component species of each group usually differed greatly in external appearance. On the other hand, certain species very similar externally show striking differences in the genitalia (*e. g.*, *N. melanderi* and *N. halophilus*). The obvious similarities are indicated in the discussions of the individual species.

The paratypes of new species herein described have been deposited in the Snow Entomological Museum at the University of Kansas and in the collection of the institution or person from whom they were borrowed. Where several paratypes were designated, pairs have been deposited in various other institutions including the United States National Museum.

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MALE GENITALIA

(Figs. 10, 11, and 12)

Techniques. Having been removed from the specimen, the genitalia were placed in a ten-percent solution of KOH and left overnight. They were rinsed in distilled water and placed in glycerin. For preservation they were kept in a microvial containing glycerin and attached to the pin of the corresponding specimen. For study it was found necessary to separate the genital capsule from the terga which form a flap over the capsule. It was not necessary to remove the aedeagus from the gonocoxites. So doing often resulted in damage to certain parts because of the small size of the genitalia.

Description. The gonocoxites are fused both dorsally and ventrally, the ventral fusion being much broader. From the base of the dorsal side of the gonocoxites there extends basally a pair of long fingerlike apodemes. On each side of these apodemes, and sometimes between them, the gonocoxites are widely emarginate. Each of these emarginations may be completely or partially filled by a thin lamella (basal lamella of gonocoxites). The absence or extent of these lamellae is a useful character in determining certain species. The gonostyli are freely articulated to the latero-posterior portion of the gonocoxites. Mesal to the gonostyli and forming dorsoventral bridges adjacent to them are a pair of stylus-like processes extending apically. The posterior margin of the ventral gonocoxal bridge may be deeply or shallowly emarginate.

The aedeagus consists of two main branches: a dorsal process and the aedeagus proper. The dorsal process is bifid distally in all species of this subgenus. It is attached to the dorsal gonocoxal bridge by a narrow membrane. The ventral branch or aedeagus proper consists of three lobes: a median penis and two lateral lobes, here called penis valves. The latter are membranous like the penis except in one species (*N. jamesi*) in which they appear sclerotized and pincerlike (Fig. 17b). At the base of the aedeagus is the aedeagal apodeme, which varies in length according to species.

TAXONOMIC SECTION

The genus *Nemotelus* of North America was revised by Melander (1903), who suggested the possible significance of vein R₄₊₅ when he noted its unforked condition in certain species. Enderlein

(1936) divided the genus and placed *N. nigrinus* Fallén, the only European species without the anterior branch of vein R_{4+5} , in a separate genus, *Nemotelinus*. Because this name was preoccupied in the family Staphylinidae of Coleoptera, Lindner (1938) published the name *Melanonemotelus* as a subgenus of *Nemotelus* to include *N. nigrinus*.

The genus *Nemotelus* has been divided according to the following combinations of characters: vein R_{4+5} forked (R_4 and R_5 present and separate distally), and males with mostly whitish abdomen (*Nemotelus s. str.*); vein R_{4+5} not forked (only R_5 present distally), and males nearly entirely black (*Melanonemotelus*). While these combinations of characters apply well to the European species, they fail to hold up when all of the North American species are considered. *N. (Nemotelus s. str.) bruesi* Melander and *pallipes* Say are both black but have vein R_{4+5} forked. *N. (Melanonemotelus) flavicornis* Johnson and *slossonae* Johnson both have mostly whitish abdomens in the males, but vein R_4 is not forked.

A study of the male genitalia substantiates the significance of the nature of vein R_4 in defining the subgenera. In all forms in which vein R_4 is simple, the dorsal process of the aedeagus (Fig. 10) is well developed and has two apical prongs. Examination of several species having vein R_4 forked, revealed that the dorsal process of the aedeagus had no apical prongs. Besides North American species, forms from Europe, Central America and South America were examined.

KEY TO SUBGENERA OF *Nemotelus* GEOFFROY

- Vein R_4 present (vein R_{4+5} forked distally); dorsal process of aedeagus without apical prongs *Nemotelus (s. str.)*
 Vein R_4 absent (vein R_{4+5} not forked distally) (Fig. 9); dorsal process of aedeagus with apical prongs (Fig. 12) *Melanonemotelus* Lindner

Subgenus NEMOTELUS Geoffroy

Nemotelus Geoffroy, 1762, Histoire abrégée des Insectes qui se trouvent aux environs de Paris, dans laquelle ces animaux sont rangés suivant un ordre méthodique. Paris, Durand, vol. 6, p. 542.

Nemotela Latreille, 1796, Précis des caractères des Insectes disposés dans l'ordre naturel, p. 164.

Nematotelus Osten Sacken, 1863, Cat. of Desc. Dipt. of N. Amer., Amer., Smithson. Inst. Misc. Coll., vol. 16, p. 48. Type species: *Musca pantherina* Linnaeus, 1758.

A key to the North American species of this subgenus has been presented by James (1936).

Subgenus MELANONEMOTELUS Lindner

- Nematotelus* Seguy, 1926, Faune de France. Paris, No. 13, p. 30. (*nec Nematotelus* Osten Sacken, 1863.)
- Nematolinus* Enderlein, 1936, Zweiflügler Diptera. Die Tierwelt Mitteleuropas. Leipzig, vol. 6, teil 3, p. 79 (type species: *Nemotelus nigrinus* Fallén, 1817; monobasic.)
- Melanonemotelus* Lindner, 1938, Die Fliegen der Palaearktischen Region. Stuttgart, E. Schweizerbart'sche verlagsbuchhandlung, vol. 4, p. 107 (type species: *Nemotelus nigrinus* Fallén, 1817; monobasic.).

The body surface in this subgenus is shining black, often with a bluish or greenish iridescence. The mesonotum is rugulose, especially toward the lateral margins, but in some species it may be completely smooth and highly polished. The pile is usually short and inconspicuous, but may be long and dense in some species, especially on the dorsum of the thorax. The facial prominence varies in length, but less so than in *Nemotelus* (*s. str.*). Two creamy-white spots are present on the frons in several species. The antennae are situated noticeably higher up on the facial prominence than in *Nemotelus* (*s. str.*) and vary little in form. In the smaller species they are usually shorter and more compact. In one species (*glaber*) the basal segments are typically yellowish. The absence of vein R_4 in the wing is the most distinctive character.

In the following key it will be noted that certain couplets apply only to males (couplets 9-15, 20, and 25). Good external characters being very few in this subgenus, it was found necessary to use such difficult characters as length and abundance of pile and relative length of the facial prominence. The latter is measured from its apex diagonally toward the nearest margin of the eye. The pile in the female is usually considerably shorter than in the male; thus, couplet 16 may be difficult to use.

KEY TO THE SPECIES OF THE SUBGENUS MELANONEMOTELUS OF AMERICA
NORTH OF MEXICO.

- | | |
|--|--------------------|
| 1. Humeral callus with at least anterior half black..... | 6 |
| Humeral callus with less than anterior half black, may be entirely yellowish white | 2 |
| 2. Abdomen wholly black | <i>tenuistylus</i> |
| Abdomen whitish or with a pale yellow lateral line on each side..... | 3 |
| 3. Thorax bare or nearly so, hairs of dorsal anterior part separated by length of a hair or more; male with abdomen mostly whitish (Florida) | 4 |
| Thorax with conspicuous pile, hairs of dorsal anterior part separated by much less than length of a hair; male with abdomen mostly black | 5 |

4. Thorax shining black; middle tibiae brown; humeral callus with anterior corners black *slossonae*
 Thorax with distinct blue iridescence; middle tibiae yellow; humeral callus wholly creamy white *flavicornis*
5. Apices of abdominal terga five and six black, not creamy white; length of facial prominence less than one third width of eye; female with large postocular creamy white spot *lambda*
 Apices of abdominal terga five and six creamy white; length of facial prominence at least one third width of eye; female without creamy white postocular spot *albimarginatus*
6. Frons with two creamy white or buff spots, contiguous in male 7
 Frons immaculate or with dark brown spots 16
7. Hind tibiae mostly yellowish, with only narrow black band around mesal portion; abdomen with thin, pale yellow lateral line on each side; large species *canadensis*
 Hind tibiae black, at most with the bases and apices yellowish; abdomen without pale yellow lateral line on each side 8
8. All tibiae entirely black except for brownish extremities; body color shining black *tristis*
 Fore and middle tibiae yellowish; body color black, usually with bluish or greenish iridescence 9
9. Pile on dorsum of thorax long over entire surface 10
 Pile on dorsum of thorax mesally very short and inconspicuous, much longer near margins of mesonotum 12
10. Male: Pile on dorsum of thorax very fine, long but inconspicuous, erect or nearly so, whitish; posterior half of humeral callus creamy white as seen from dorsal aspect; gonocoxal ventral bridge not deeply emarginate, but with an apparent double notch in posterior margin, gonostyli curved, with blunt apices (Fig. 29) ... *communis*
 Male: Pile on dorsum of thorax shining and conspicuous, sometimes giving a "shaggy" appearance, often with a buff tinge; humeral callus usually mostly black; gonocoxal ventral bridge deeply emarginate, without an apparent double notch; gonostyli either curved and with sharp apices, or straight and with blunt apices (Figs. 15, 16, and 18) 11
11. Gonostyli strongly curved, apices pointed (Fig. 16c) (Distribution mainly Great Basin and Rocky Mountain regions) *politus*
 Gonostyli straight or only slightly curved, apices rounded, blunt (Fig. 18c) (Distribution mainly west of Sierra Nevada and south along Pacific coast) *arator*
12. Knobs of halteres chalky white 13
 Knobs of halteres pale yellowish buff or partly brown 15
13. Male: Gonocoxites with basal lamellae absent or only slightly evident (Fig. 14) *politus*
 Male: Gonocoxites with basal lamellae complete (Figs. 19 and 20) .. 14
14. Penis valves black, pincerlike, sclerotized (Fig. 19) *jamesi*
 Penis valves transparent, membranous, narrow and inconspicuous (Fig. 20) *variabilis*

15. Knobs of halteres wholly pale yellowish buff, sometimes paler beneath (Atlantic Coast)	<i>sabroskyi</i>
Knobs of halteres with clearly defined brown or buff blotch restricted to dorsoposterior area	<i>picinus</i>
16. Dorsum of thorax with pubescence over entire surface, but often extremely short and inconspicuous mesally especially in female; at least a few hairs immediately anterior to scutellum	17
Dorsum of thorax bare mesally, sometimes with a few very short hairs anteriorly, but never immediately anterior to scutellum	21
17. Facial prominence of male less than one third width of eye (Fig. 8a); small species, about 3 mm. in length	18
Facial prominence of male at least one third width of eye as seen from lateral aspect (Figs. 1 and 4); length 3.5 mm. or longer . . .	19
18. Abdomen with buff or light yellow lateral line on each side, these lines very thin in female; basal lamellae of gonocoxites absent (Fig. 23)	<i>halophilus</i>
Abdomen without buff lateral lines; basal lamellae of gonocoxites complete (Fig. 22)	<i>melanderi</i>
19. Facial prominence very long, its length in male half of width of eye viewed laterally; its length in female about equal to width of eye; frons never with spots (Fig. 1)	<i>beameri</i>
Facial prominence not noticeably long and tapering, its length in male less than half the width of eye viewed laterally; its length in female less than width of eye; frons with or without brown spots (Fig. 4)	20
20. Dorsal process of aedeagus with apical prongs convergent; base of aedeagus strongly curved (Fig. 20) (southern species, California to Florida and into Mexico)	<i>variabilis</i>
Dorsal process of aedeagus with apical prongs divergent; base of aedeagus not strongly curved (Fig. 21) (Great Lakes region west to South Dakota)	<i>centralis</i>
21. All tibiae completely black or dark brown	<i>glaber</i>
Fore tibiae at least partly yellow	22
22. At least basal segments of antennae yellow or yellowish brown . . .	23
Antennae wholly black or dark brown	24
23. Gonostyli with strongly curved outer edges, apices pointed; penis valves pointed; gonocoxal apodemes short, convergent (Fig. 14). Knobs of halteres with brown or buff blotch only on dorsal half	<i>glaber</i>
Gonostyli slightly curved, not so sharply pointed; penis valves truncated, widest at apices; gonocoxal apodemes long, parallel (Fig. 30); knobs of halteres with dorsal brown or buff blotch nearly covering distal end	<i>picinus</i>
24. Knobs of halteres partly brownish or entirely white; aedeagus brown, sclerotized, the penis and penis valves forming three well-separated prongs (Fig. 13); facial prominence of female as long as width of eye or nearly so, as seen from lateral aspect (some <i>beameri</i> females may key out here. Compare Figs. 1b and 2b)	<i>nigrinus</i>

- Knobs of halteres always partly brownish; aedeagus membranous, penis and penis valves contiguous; facial prominence of female short, about half as long as width of eye as seen from lateral aspect 25
25. Basal lamellae of gonocoxites large, extending nearly to apices of apodemes; penis merely a short lobe between penis valves (Fig. 21) *centralis*
- Basal lamellae of gonocoxites absent, apodemes long, parallel; penis long, longer than prongs of dorsal process (Fig. 30) *pinus*

Nemotelus nigrinus Fallén

(Figs. 2, 13)

- Nemotelus nigrinus* Fallén, 1817, Diptera Sveciae, vol. 6, p. 3; Meigen, 1822, Syst. Beschreib. der bekannten Eur. Zweiflüg. Insecten, vol. 3, p. 1175; Macquart, 1934, Hist. Nat. des Ins. Dipteres, vol. 1, p. 266; Zetterstedt, 1842, Dipt. Scand., vol. 1, p. 151; Walker, 1851, Insecta Britannica, vol. 1, p. 26; Schiner, 1862, Fauna Austriaca, Die Fliegen, vol. 1, p. 5; Siebke, 1874, Insectorum Norvegicorum, fasc. 1, p. 7; Van der Wulp, 1877, Diptera neerlandica, p. 447; Aldrich, 1905, Cat. N. Amer. Diptera, Smithson. Inst. Misc. Coll., vol. 46, p. 190; Lundbeck, 1907, Diptera Danica, part 1, p. 30; Verrall, 1909, Brit. flies, vol. 4, p. 125; Seguy, 1926, Faune de France, no. 13, p. 30; James, 1951, Proc. Ent. Soc. Wash., vol. 53, p. 343.
- Nemotelus carneus* Walker, 1849, List of the Specimens of Dipterous Insects in the Collection of the British Museum, part 3, p. 521; Melander, 1903, Psyche, vol. 10, p. 178; Aldrich, 1905, Cat. N. Amer. Diptera, Smithson. Inst. Misc. Coll., vol. 46, p. 190 (new synonymy).
- Nemotelus crassus* Loew, 1861, Diptera Americae Septentrionalis Indigena, Cent. III, p. 109; Williston, 1885, Can. Ent., vol. 17, p. 128; Melander, 1903, Psyche, vol. 10, p. 175; Aldrich, 1905, Cat. N. Amer. Diptera, Smithson. Inst. Misc. Coll., vol. 46, p. 190; Curran, 1927, Roy. Soc. Canada, Trans., sect. 5, vol. 21, p. 225 (new synonymy).
- Nemotelus unicolor* Loew, 1861, Diptera Americae Septentrionalis Indigena, Cent. III, p. 109; Williston, 1885, Can. Ent., vol. 17, p. 128; Melander, 1903, Psyche, vol. 10, p. 176; Aldrich, 1905, Cat. N. Amer. Diptera, Smithson. Inst. Misc. Coll., vol. 46, p. 190; Curran, 1927, Roy. Soc. Canada, Trans., sect. 5, vol. 21, p. 224; Leonard, 1928, Cornell Agric. Expt. Sta., Mem. 101, p. 753; Knowlton, 1931, Can. Ent., vol. 63, p. 153 (new synonymy).
- Nemotelus carbonarius* Loew, 1865, Diptera Americae Septentrionalis Indigena, Cent. VIII, p. 119; Melander, 1903, Psyche, vol. 10, p. 177; Aldrich, 1905, Cat. N. Amer. Diptera, Smithson. Inst. Misc. Coll., vol. 46, p. 190; Leonard, 1928, Cornell Agric. Expt. Sta., Mem. 101, p. 753 (new synonymy).

This is a widespread northern European and northern North American species. Although the type was not examined by this author, several specimens from England and northern Sweden were available and their genitalia were examined. The form known as *unicolor*, which is widespread in Canada, Alaska, and northern United States, shows no significant differences, either externally or in the genitalia, from European *nigrinus*, except that in some specimens the knobs of the halteres are somewhat darkened. The type of *carbonarius*, although smaller, has genitalia identical with *ni-*

grinus. Its halteres are darkened, unlike typical *nigrinus*, and the thoracic lateral lines are almost obliterated. However, intermediate conditions between the two are frequently encountered, and no distinct line of separation was found possible. The type of *crassus*, a female, appears to be merely a slight variant of *nigrinus* with the second antennal segment yellowish apically. In all other respects it is like *nigrinus*, which cannot be confused with other species found in Rhode Island, the type locality of *crassus*. The type of *carneus*, also a female, was not available to the author, but the description agrees with that of *nigrinus*, and the type locality (St. Martin's Falls, Albany River, Ontario) is within the range of only that species.

In general, the body proportions, especially in the head, are between *beameri* and *pycinus*, but some individuals approach or equal these species in this respect. Examination of the male genitalia is usually necessary for determination. However, the bare mesal portion of the dorsum of the thorax distinguishes it from *beameri* males, and the wholly black or dark brown antennae nearly always distinguishes it from *glaber*, in which the basal segments are yellow or yellowish brown.

Male: Body color shining black, usually with bluish iridescence on facial prominence and frons. Facial prominence moderately long (Fig. 2a); frons without pale spots; antennae brownish black to black. Thorax with rather sparse, white pile, becoming bare toward mesal portion of mesonotum; scutellum nearly bare; mesonotum with yellowish lateral margins forming a thin line on each side; humeral calli with small yellowish spot above each spiracle. Knobs of halteres white (in some specimens ranging from tan to dark brown on apical portions). Femora black with yellow apices; fore and middle tibiae yellow, hind tibiae mostly black with yellow bases and apices; tarsi pale yellow, apical segments brownish. Abdomen concolorous with thorax, but less pilose. Gonostyli with outer edges curved subapically; emargination of ventral bridge of gonocoxites V-shaped; apodemes short; basal lamellae moderately developed, covering nearly half of emarginations; aedeagus fork-like, the penis valves pointed, more or less straight but directed slightly mesad; penis shorter than, and distinctly separated from penis valves from point of junction. Length, 3.5-4.5 mm.

Female: Like male except for sexual differences in head: eyes smaller, separated; facial prominence longer (Fig. 2b).

Distribution: ARIZONA: Oak Creek Canyon. CALIFORNIA: Lone Pine, Inyo Co.; Tejon Canyon, Kern Co.; White Mountains, Mono

CO. COLORADO: Florissant; Gold Hill; Grant. IDAHO: Bloomington; Cub River Canyon; Moscow; Paris. ILLINOIS: Algonquin; Calumet; Carbondale; Gary; Chicago; Elburn; St. Joseph; Urbana; White Heath. INDIANA: Chesterton; Hammond; Lafayette. IOWA: Alleman; Ames; Polk City; Sioux City. KANSAS: Douglas Co.; Muscotah; Sun City. MASSACHUSETTS: Beverly. MICHIGAN: Bay City; Detroit; East Lausang; Eaton Rapids; Hemlock; Saginaw Co.; Livingston Co.; Mason; Salem; Traverse City; Vandalia. MINNESOTA: Beltrami; Clear River; Eagle Bend; Grand Rapids; Houston Co.; Itasca Park; John Latch State Park, Winona Co.; Mantorville; Minneapolis; Owatonna; Plummer; Ramsay Co.; St. Anthony; St. Peter. MISSISSIPPI: "Agricultural College." NEBRASKA: Kayapaha Co.; Valentine. NEW HAMPSHIRE: (no specific locality). NEW JERSEY: Mullica Hill. NEW MEXICO: Moriarty. NEW YORK: Slaterville; Caroline. SOUTH DAKOTA: Big Stone City; Canton. UTAH: Hayden; Holt; Kelton; Smithfield. WISCONSIN: Dane Co. WYOMING: Burntfork; S. Pass City. ALBERTA: Banff; Laggan. BRITISH COLUMBIA: 290 miles. MANITOBA: Fort Churchill, Hudson Bay Ry. mile 505; Sundown. NORTHWEST TERRITORIES: Saw Mill Bay. ONTARIO: Orillia; Ottawa; Sandford; Simcoe; Toronto; Trenton. QUEBEC: Abbotsford; Aylmer; Montreal; Outrem't; Rupert House. YUKON TERRITORY: Whitehorse. ALASKA: Fairbanks; Matanuska Valley.

The location of the type of *nigrinus* is unknown to the author, that of *carneus* from St. Martin's Falls, Albany River, Ontario, is in the British Museum, that of *crassus* from Rhode Island, that of *unicolor* from Illinois, and that of *carbonarius* from Lenox, Massachusetts, are in the Museum of Comparative Zoology at Harvard University.

Flight records: March 18 (Mississippi) to July 29 (Wyoming).

Nemotelus glaber Loew

(Figs. 4, 14)

Nemotelus glaber Loew, 1872, *Diptera Americae Septentrionalis Indigena*, Cent. X, p. 232; Melander, 1903, *Psyche*, vol. 10, p. 177; Aldrich, 1905, *Cat. N. Amer. Diptera*, *Smithson. Inst. Misc. Coll.*, vol. 46, p. 190; Curran, 1927, *Roy. Soc. Canada, Trans.*, Sect. V, vol. 21, p. 224.

Nemotelus flavicornis James, 1932 (not Johnson, 1894), *Amer. Mus. Nov.*, no. 517, p. 7 (new synonymy).

Nemotelus fulvicornis James, 1936, *Bull. Brooklyn Ent. Soc.*, vol. 31, p. 86 (new name for *flavicornis* James) (new synonymy).

This species has two forms; one with nearly entirely black legs, the other with extensive yellow areas on tibiae and fore femora. No intergrades have been found. Both occur throughout the range

which extends from Michigan and New York, southwestward into Mexico, and both have been taken together by this author. The type of *glaber* belongs to the black-legged form, but the yellow-legged form appears to be more common. *Fulvicornis*, the holotype of which is a female, has the typical orange-tan base of the antennae and olive-tinged thorax of *glaber* and is here regarded as a synonym. Should the yellow-legged form prove to be a distinct species, the name *fulvicornis* is available for it. The dorsum of the thorax is nearly bare. The body proportions are like those of *pycinus* and *centralis*, and it is smaller and has a shorter facial prominence than most *nigrinus* individuals.

Female: Body color shining black with olive tinge, especially on dorsum of thorax. Facial prominence moderately short, stout (Fig. 4a); frontal spots absent; antennae short, compact, yellowish brown except for brownish black terminal pseudosegment. Thorax nearly bare, pubescence at margins of dorsum short, sparse, absent mesally. Mesonotum with thin pale yellow line on each lateral margin extending onto humeral callus. Femora and tibiae black, the apices with very small yellowish areas; apical two segments of fore tarsi and apical segments of middle and hind tarsi infuscated, otherwise pale yellow. Halteres with knobs white, each with brown blotch dorsally, covering about half of distal end. Abdomen concolorous with thorax. Length, 3.3 to 3.5 mm.

Male: Like female except for the usual sexual differences in head (Fig. 4b). Genitalia small; gonostyli strongly and evenly curved, with pointed apices; emargination of ventral bridge of gonocoxites deep, nearly evenly rounded; apodemes convergent; basal lamellae small; aedeagus similar to that of *nigrinus* but smaller, penis valves more blunt and slightly convergent (Fig. 14). Length, 3.3 mm.

Distribution: ILLINOIS: Dubois; Homer; Monticello; Odin; St. Joseph; Urbana; White Heath; Winchester. INDIANA: Lafayette. IOWA: Lacey-Keosauqua State Park, Van Buren Co.; Lewis and Clark State Park, Monona Co.; Onawa. KANSAS: Lawrence; Muscotah Marsh. LOUISIANA: Mound; Opelousas; Shreveport. MICHIGAN: Detroit; Saugatuck. MISSISSIPPI: "Agricultural College." MISSOURI: Columbia; Jefferson City. NEW YORK: Babylon; Long Island. OHIO: Summit Co.; Amherst. TEXAS: Brownsville; College Station; Dallas; Devil's River; Harlingen; New Brunswick; Victoria. VIRGINIA: Potomac Creek. GUERRERO: Acapulco. MORELOS: Cuernavaca. SAN LUIS POTOSI: Pujal; Xilitla.

Holotype, female: Texas, in the Museum of Comparative Zoology at Harvard University; that of *fulvicornis*, female, from Lawrence, Kansas, is in the American Museum of Natural History.

Flight records: March 17 (Brownsville, Texas) to September 27.

Nemotelus canadensis Loew

(Figs. 3, 15)

Nemotelus canadensis Loew, 1861, *Diptera Americae Septentrionalis Indigena*, Cent. III, pp. 109, 110; Melander, 1903, *Psyche*, vol. 10, p. 175; Aldrich, 1905, *Cat. N. Amer. Diptera*, *Smithson. Inst. Misc. Coll.*, vol. 46, p. 189; Curran, 1927, *Roy. Soc. Canada, Trans.*, sect. V, vol. 21, p. 225; Leonard, 1928, *Cornell Agric. Expt. Sta., Mem.* 101, p. 753; Knowlton, 1931, *Can. Ent.*, vol. 63, p. 153.

This widespread species is related to *arator* and *politus*. It is distinguished by the thin lateral yellowish abdominal lines and the narrow black band around the mesal portion of the hind tibiae.

Male: Body color shining black with olivaceous tinge. Facial prominence moderately long, stout (Fig. 3a). Frontal spots pale yellow, contiguous. Antennae brownish black. Thorax densely pilose, the hairs very long, erect, shining white with slight yellow tinge, slightly longer near edges of mesonotum; mesonotum with lateral margin narrowly pale yellow; humeral calli with yellow spot covering less than one half dorsal surface. Halteres with knobs white. Femora black with yellow apices; fore and middle tibiae yellow, hind tibiae with narrow black transverse median band covering less than one third length of tibiae; tarsi pale yellow, the apical segments slightly infuscated. Abdomen concolorous with thorax, less pilose; third, fourth, and fifth abdominal terga narrowly margined laterally with pale yellow; gonostyli with curved lateral edges, apices sharply pointed; gonocoxites with ventral bridge deeply emarginate; aedeagus membranous, the penis valves pointed, longer than penis (Fig. 15). Length 4-5 mm.

Female: Like male except for shorter pile and the usual sexual differences in head. Length 4-5 mm.

Distribution: This species is widely distributed in the following localities: NORTHWEST TERRITORIES: Fort Resolution; Hyarling River. ALBERTA: Lethbridge; Medicine Hat; Taber, Chin; Coaldale. BRITISH COLUMBIA: One Hundred Mile House; Oliver. MANITOBA: Balduf; Russel. SASKATCHEWAN: Little Quill; Pleasant Creek. ALASKA: Anchorage; Matanuska. CALIFORNIA: Spaulding, Lassen Co.; Lompoc. COLORADO: Roggen. IDAHO: Geneva; Henry, Caribou Co.; Montpelier. MINNESOTA: Douglas Co.; Willmer.

MONTANA: (no specific locality). NEVADA: Wells. NORTH DAKOTA: Turtle Mountains. UTAH: Altonoto; Blue Creek; Brigham; Ephraim; Fielding; Garden City; Garland; Goshen; Hyde Park; Logan; Magna; Manti; Mona; Myton; Sage Junction; Salt Lake City; Slaterville; Smithfield; Spanish Fork; Trenton; Vernal; Wellsville; Woodside. WASHINGTON: Harrah; Roche Harbor; Sunnyside; Toppenish; Yakima. WYOMING: Yellowstone National Park.

The types, from Fort Resolution, N. W. T., are in the Museum of Comparative Zoology at Harvard University.

Flight records: May 1 to September 7.

Nemotelus politus sp. nov.

(Fig. 16)

Nemotelus simplex Snow, 1904, Univ. Kansas Sci. Bull., vol. 2, no. 12, p. 341 (*nomen nudum*).

This species is related to *arator* and *canadensis* which it closely resembles, especially in the form of the genitalia (compare Figs. 15, 16 and 18). It is often difficult to distinguish from *communis*, especially the females. However, the pilosity is different, that of *communis* being thinner, less conspicuous, and the hairs more evenly spaced.

Male: Body color shining black with slight bluish iridescence. Facial prominence moderately long, as in *communis* (Fig. 6a); frons with two pale yellow contiguous spots; antennae brownish black. Thorax rather densely pilose, the hairs silvery white, suberect, longer near margins of mesonotum, long on scutellum. Mesonotum with lateral margins pale yellow; humeral calli with pale yellow spot above each mesothoracic spiracle, covering about one third of each callosity (in a few specimens observed about half of callosity is pale yellow). Knobs of halteres white. Femora black with yellow apices; fore and middle tibiae yellow, hind tibiae mostly black with yellow bases and apices; tarsi pale yellow, apical segments slightly infuscated. Abdomen concolorous with thorax, less pilose, the hairs shorter and sparser than those on thorax. Gonostyli with curved outer edges, the apices sharply pointed; ventral bridge of gonocoxites deeply emarginate at apical margin; penis valves somewhat pointed, longer than penis (Fig. 16). Length, 4-4.5 mm.

Female: Like male except for sexual differences in head; pilosity on dorsum of thorax shorter. Length, 4-4.5 mm.

Distribution: CALIFORNIA: Deep Spring, Inyo Co.; Kern Co.; Owen's Valley, Inyo Co.; Paradise Spring, Monterey Co.; Sardine

Creek, Mono Co.; Victorville, San Bernardino Co. IDAHO: Mesa; Middleton; Nampa; Star; Wilder. MONTANA: (no specific locality). NEVADA: Austen; Fallon; Reno. OREGON: Elgin. UTAH: Allen Canyon; American Fork; Blue Creek; Brigham; Duchesne; Ephraim; Farmington; Garland; Heber; Hooper; Huntsville; Layton; Logan; Mapleton; Midvale; Morgan; Pintura; Promontory; Smithfield; Vernal. WASHINGTON: Walla Walla. WYOMING: South Pass City.

Holotype, male: Midvale, Utah, Aug. 7, 1937 (Knowlton); allotype, female: Huntsville, Utah, June 8, 1938 (Knowlton and Hardy), both in the Snow Entomological Museum at the University of Kansas. Paratypes (six males, two females): Logan, Utah, June 5 and 7, 1939 (G. F. Knowlton and G. S. Stains); American Fork, Utah, Aug. 23, 1936 (G. F. Knowlton); Mapleton, Utah, June 16, 1937 (G. F. Knowlton); Pintura, Utah, August 11, 1929 (R. H. Beamer); Wilder, Idaho, June 27, 1945; Clarkston, Utah, June 10, 1944 (S. L. Wood); Huntsville, Utah, June 27, 1937 (G. F. Knowlton); Middletown, Idaho, July 19, 1944 (W. E. Shull); Fallon, Nevada, Aug. 12, 1940 (L. J. Lipovsky); Blue Creek, Utah, June 3, 1954 (G. F. Knowlton); Vernal, Utah, June 29, 1954 (G. F. Knowlton).

Flight records: April 4 (Monterey Co., California) to August 12 (Nevada).

Nemotelus arator Melander

(Fig. 18)

Nemotelus arator Melander, 1903, *Psyche*, vol. 10, p. 179; Aldrich, 1905, *Cat. N. Amer. Diptera*, Smithson. Inst. Misc. Coll., vol. 46, p. 189; Curran, 1927, *Roy. Soc. Canada, Trans.*, sect. V, vol. 21, p. 225.

The commonest species of California west of the Sierra Nevada Mountains, this species is similar to *politus*, to which it is closely related. Most individuals have a greenish tinge, and the gonostyli are straight and blunt, while *politus* has gonostyli with curved lateral edges and pointed apices. Another similar species, *canadensis*, has lateral abdominal stripes which this species lacks. The types were not seen by the author; however, several topotypical paratypes were available and agree with Melander's description of the species.

Male: Body color shining olivaceous to bluish black. Facial prominence moderately long, as in *communis* (Fig. 6a); frons with two pale yellow contiguous spots; antennae brownish black. Thorax covered with rather long, dense, pale yellow to white pile, longer at lateral margins of mesonotum and on scutellum. Mesonotum

with lateral margins pale yellow, forming a narrow line on each side; humeral calli with small, pale yellow spot above each mesothoracic spiracle. Knobs of halteres white. Femora black with yellow apices; fore and middle tibiae yellow, hind tibiae mostly black with yellow bases and apices; tarsi pale yellow; apical segments slightly infuscated. Abdomen concolorous with thorax, less pilose. Gonostyli straight, rounded at apices; aedeagus as in *politus* (Fig. 16). Length, 4.5 mm.

Female: Like male except for sexual differences in head; pilosity of dorsum of thorax shorter. Length, 4.5 mm.

Distribution: CALIFORNIA: Albany, Alameda Co.; Antioch; Bolinas; Claremont; Davis; Fairfax; La Jolla; Los Angeles; Modoc Co.; Monterey Co.; Mt. Diablo; Palo Alto; Pomona; Pt. Reyes, Marin Co.; Redwood City; Rio Vista; San Diego Co.; Santa Clara Co.; Sardine Creek, Mono Co.; Tolay Creek, Sonoma Co.; Tracy, San Joaquin Co.; Ventura Co.; Yolo Co. WASHINGTON: Kennewick; Prosser; Walla Walla.

Holotype and allotype: San Diego County, California, in the Melander collection, Riverside, California.

Flight records: March 5 (San Diego Co., California) to August 31 (Sonoma Co., California).

Nemotelus tristis Bigot

(Fig. 17)

Nemotelus tristis Bigot, 1887, Ann. Soc. Ent. France, ser. 6, vol. 7, p. 30.
Melander, 1903, Psyche, vol. 10, p. 177.

I have not seen the type, but although the original description is extremely brief, the combination of pale frontal spots and nearly completely black legs leaves little doubt as to the identity of this species.

The black, nonmetallic coloration of this species and the wholly black femora and tibiae distinguish it from the closely related *canadensis*, *arator* and *politus*, which have very similar male genitalia but possess extensive yellow areas on the legs.

Male: Body color shining black. Facial prominence moderately long (Fig. 6a); frontal spots creamy white, contiguous; antennae black. Thorax with rather dense white pile covering entire dorsum, longer near lateral margins, much shorter on scutellum; mesonotum with lateral margins narrowly yellow, forming a very thin line on each side. Each humeral callus with small yellow spot above mesothoracic spiracle. Femora black, tipped with yellowish brown; tibiae entirely black except for small yellowish brown areas at

bases and apices; tarsi with basal segments yellowish brown, the remaining segments progressively blacker toward apices. Halteres with knobs pale creamy white. Squamae slightly infuscated. Abdomen concolorous with thorax, pile less dense. Gonostyli with evenly curved outer edges, apices pointed; aedeagus with penis valves pointed, longer than penis (Fig. 17). Length, 4-5 mm.

Female: Like male except for shorter, more appressed pile on thorax and the usual sexual differences in head. Length, 4.8 mm.

Distribution: CALIFORNIA: Davis; Mt. Hamilton, Santa Clara Co.; Oakhurst, Madera Co.; Panoche Creek, Fresno Co.; Putah Canyon, Yolo Co.; Woody, Kern Co.

Types: Bigot apparently described this species from a series of two males and two females collected in California and now in the care of Mr. J. E. Collin in England. Both of the males are damaged, and according to Mr. Collin, one appears to represent a distinct species from the other three specimens in having pale fore and middle tibiae.

Flight records: March 26 to June 8.

Nemotelus jamesi sp. nov.

(Fig. 19)

This species closely resembles a few other species within its range, especially *arator* and *politus*. However, the male genitalia are strikingly different in that the penis valves are sclerotized and sharply pointed in this species. The form of the genital capsule and strong curvature of the aedeagus indicates a close relationship with *variabilis*, a more southern species. The females are without, or with only minute, frontal spots.

Male: Body color shining black with slight bluish iridescence. Facial prominence moderately long (Fig. 6a); frontal spots pale yellow, small, contiguous; antennae brownish black. Thorax with moderately dense pilosity near margins of mesonotum, becoming sparse, short, and sub-appressed mesally; lateral margins narrowly pale yellow; each humeral callus with small pale yellow spot above mesothoracic spiracle covering less than one third of dorsal surface. Femora black with yellow apices; fore and middle tibiae yellow, slightly infuscated; hind tibiae mostly black with yellow apices and more extensively yellow bases; tarsi pale yellow, apical segments infuscated. Halteres with knobs white. Abdomen concolorous with thorax, but less pilose. Gonostyli with apical portions bent inward; penis valves black, sclerotized, pincerlike. Aedeagus strongly curved dorsally (Fig. 19).

Female: Like male except for absence of frontal spots, facial prominence longer, eyes smaller, pubescence shorter.

Distribution: CALIFORNIA: Escondido; Hallelujah Junction, Lassen Co. IDAHO: Fish Haven. NEBRASKA: Norway; Valentine. UTAH: Logan Dry Canyon; Thatcher; Yost. WASHINGTON: Prosser.

Holotype, male, and allotype, female: Prosser, Washington, May 2, 1951 in the collection of the State College of Washington. Paratypes: ten males, nine females, same data as holotype.

Flight records: May 2 to Aug. 25.

Nemotelus variabilis sp. nov.

(Fig. 20)

This widespread southern species ranges from California to Florida. It varies greatly in size and in coloration; the frontal spots are usually absent but are present in some individuals. The genitalia are similar to those of *jamesi* in that the aedeagus is strongly curved, but differ in being considerably narrower.

Male: Body color shining black with bluish iridescence. Facial prominence relatively short (Fig. 4a). Frontal spots absent. (In some, small yellowish or brownish spots are present.) Antennae brown, basal two segments yellowish brown. Thorax with pile short over entire dorsum, very short mesally, longer near lateral margins, short on scutellum. Mesonotum with lateral margins narrowly yellowish tan. Each humeral callus with small yellow spot above mesothoracic spiracle. Halteres with knobs pale buff (white in some). Femora black with yellow apices; fore and middle tibiae yellow, slightly infuscated; hind tibiae black medially with yellow bases and apices; (in some individuals each hind tibia has a narrow medial black band); tarsi pale yellow. Abdomen concolorous with thorax. Gonostyli curved; ventral bridge of gonocoxites strongly convex and deeply emarginate at basal margin; basal lamellae complete, extending nearly to apices of adopedemes. Aedeagus strongly curved; prongs of dorsal process convergent; penis and penis valves equal in size, very slender and inconspicuous (Fig. 20). Length, 3.5-4.2 mm.

Female: Like male except for sexual differences in head and shorter pile. Length, 3.2-4.5 mm.

Distribution: ARIZONA: Bill Williams Fork. CALIFORNIA: Arroyo R.; Cazadero; Lone Pine, Inyo Co.; Little Lake, Inyo Co.; Los Angeles; Olanche, Inyo Co.; Panamint Mountains, Inyo Co. FLORIDA: Biscayne Bay; Charlotte Harbor; Hibernia; Homestead; Sanford; St. Augustine; Yankeetown. NEVADA: Carson City. NEW

MEXICO: Laguna, Valencia Co.; Las Cruces; Mesilla Park; Roswell.
TEXAS: Anahuac; Brownsville; Hidalgo; Southmost; Victoria.
UTAH: St. George.

Holotype, male, and allotype, female: Hibernia, Florida, August 7, 1939 (R. H. Beamer), in the Snow Entomological Museum at the University of Kansas.

Paratypes: seven males, two females, Sanford, Florida, April, 1908 and 1926 (Van Duzee); Biscayne Bay, Florida (C. W. Johnson); Yankeetown, Florida, July 7, 1948 (R. H. Beamer); Hibernia, Florida, Aug. 7, 1939 (D. E. Hardy); St. Augustine, Florida; Charlotte Harbor, Florida.

Flight records: March 27 (southern Texas) to August 8 (California).

Nemotelus centralis sp. nov.

(Fig. 21)

Almost indistinguishable from *picinus* except for the genitalia, this species also has much the same range of distribution. The complete basal lamellae of the gonocoxites, the short, convergent apodemes, and the small lobelike penis distinguish it from that species, which has no basal lamellae, long parallel apodemes, and much longer penis.

Male: Body color shining black. Facial prominence as in *glaber* (Fig. 4a), shorter than in *nigrinus*, rather pointed. Frontal spots dark brown, not conspicuous. Antennae brownish black, short, compact. Thorax with short pubescence on dorsum, nearly absent mesally, longer toward margins. Mesonotum with lateral margins narrowly pale yellow. Humeral calli with small yellowish spot above each mesothoracic spiracle. Halteres with knobs brownish apically and dorsally. Femora black with about one fifth of apical portions yellow; fore and middle tibiae yellowish brown, hind tibiae with middle half black, yellow basally and apically; tarsi pale yellow. Abdomen concolorous with thorax. Genital capsule rounded as seen from dorsal aspect; apical process of gonocoxites short, thick; basal lamellae complete, extending nearly to apices of apodemes, which are short, convergent; penis valves short, together forming rounded outline, not extending beyond prongs of dorsal process; penis appearing as a small medial lobe between the longer penis valves (Fig. 19). Length, 3.4 mm.

Female. Unknown.

Distribution: ILLINOIS: Algonquin. MICHIGAN: Detroit; Douglas Lake; Midland Co. MINNESOTA: Clear River; Eagle Bend;

Wadena; Washington Co. OHIO: Summit Co. SOUTH DAKOTA: Brookings. ONTARIO: Trenton; Simcoe.

Holotype, male; Clear River, Minnesota, June 22, 1922 (Gilmer) in the collection of the University of Minnesota. Paratypes: three males, Brookings, South Dakota, and Washington Co., Minnesota, July 22, 1914; Simcoe, Ontario, June 20, 1939 (G. E. Shewell).

Flight records: June and July.

Nemotelus melanderi Banks

(Figs. 8, 22)

Nemotelus melanderi Banks, 1920, Canadian Ent., vol. 52, p. 65; Curran, 1927, Roy. Soc. Canada, Trans., sect. V, vol. 21, p. 225; Leonard, 1928, Cornell Agric. Expt. Sta., Mem. 101, p. 753.

This coastal species can easily be distinguished from other eastern species by the small size and short facial projection. In these respects it resembles very closely the southwestern species *halophilus*. However, there are great differences in the genitalia (cf. Figs. 22, 23).

Male: Body color shining brownish black. Facial prominence short (Fig. 8a) rugose, haired, with slight depression below antennae. Frontal spots absent. Antennae brownish black. Thorax with long thin pile on dorsum. Mesonotum with lateral margins yellowish brown, forming very thin lines which extend onto humeral calli above mesothoracic spiracles. Halteres with knobs ivory-white. Femora dark brown, the apices pale; tibiae brown with pale bases and apices; tarsi pale yellow. Abdomen concolorous with thorax. Genitalia small, the gonostyli curved; gonocoxal apodemes short, convergent; basal lamellae large, extending nearly to apices of apodemes; penis valves appear as small lobes on each side of penis which extends slightly beyond them (Fig. 22). Length, 3 mm.

Female: Like male except for sexual differences in head (Fig. 8b).

Distribution: FLORIDA: Paradise Key; Royal Palm Park. MARYLAND: Chesapeake Beach. MASSACHUSETTS: Beverly; Gloucester; Woods Hole. NEW JERSEY: Lake Branch; Morgan. NEW YORK: Calverton, Long Island; Cold Spring Harbor; Montauk, Long Island; Orient, Long Island; Southold. VIRGINIA: Mathias Point. NOVA SCOTIA: Baddeck; Cape Breton.

The types, twelve males, Chesapeake Beach, Maryland, two females, Bayville, New York, are in the Museum of Comparative Zoology at Harvard University.

Flight records: April 4 (Florida) to September 4 (Virginia)

Nemotelus lambda James

(Figs. 7, 24)

Nemotelus lambda James, 1933, Jour. Kansas Ent. Soc., vol. 6, pp. 70-71; 1936, Bull. Brooklyn Ent. Soc., vol. 31, pp. 86-91.

The globose head, short facial projection, and large pale markings on the head, thorax and abdomen set this species apart from all others from this area.

Male: Body color shining black with ivory-white markings. Facial prominence very short, depressed between apex and origin of antennae (Fig. 7a). Frontal spots large, ivory-white, contiguous. Antennae black. Thorax densely pilose, the hairs erect, very long over entire dorsum. Humeral calli and lateral margins of mesonotum ivory-white, the latter broad. Knobs of halteres white. Femora black with whitish apices; fore and middle tibiae yellow, hind tibiae with black middle portion and yellow bases and apices; tarsi yellowish white. Abdomen concolorous with thorax, less pilose; second, third, and fourth tergites with conspicuous lateral margins, ivory-white, obsolete on first and fifth segments; second and third sternites with lateral and posterior margins whitish. Gonostyli very pointed at apex, inner edge broadly lobate in middle region (Fig. 24); apical processes of gonocoxites shorter than gonostyli. Gonocoxites deeply emarginated on each side of basal apodemes; basal lamellae absent; basal apodemes very long, parallel. Aedeagus attached to gonocoxites by broad membrane, apical prongs of dorsal process slightly convergent (Fig. 24b). Length, 4-4.5 mm.

Female: Like male except for the following: Facial prominence short, without depression above. Eyes widely separated. Frontal spots much larger, not contiguous; posterior ocular orbits prominently ivory-colored on lower half (Fig. 7b). Thorax with pile much shorter. Abdomen with narrow but definite whitish lateral margins.

Distribution: NEW MEXICO: Albuquerque; Jemez Springs; Roosevelt County.

Holotype, male: Roosevelt County, New Mexico, July 7, 1927, in the Snow Entomological Museum at the University of Kansas. Allotype, female: Jemez Springs Mountains, New Mexico, May, in the collections of Purdue University.

Flight records: May and July.

Nemotelus halophilus sp. nov.

(Fig. 23)

Although resembling *melanderi* very closely, this species appears to be more closely related to the following two species as indicated by the genitalia (Figs. 22-27). Externally *halophilus* may be distinguished by the buff or yellow lateral abdominal line. This species has been found only near salt marshes in New Mexico and Kansas and along the gulf coast of Texas.

Male: Body color shining brownish black. Facial prominence short (Fig. 8a), haired, profile with slight depression below antennae. Frontal spots absent. Antennae brownish black. Thorax with long thin pile on dorsum. Mesonotum with lateral margins narrowly yellowish brown, forming thin lines which extend onto humeral calli above mesothoracic spiracle. Halteres with knobs white. Femora dark brown with yellowish brown apices; tibiae dark brown with yellowish brown bases and apices; tarsi pale yellow. Abdomen concolorous with thorax except that lateral margins of terga and sterna three to six are yellowish buff. Pilosity sparser than on thorax. Genitalia small; emargination of ventral bridge of gonocoxites evenly rounded, moderately deep; gonocoxal apodemes long, divergent; basal lamellae absent; aedeagus short; prongs of dorsal process pointed, divergent; penis slightly shorter than penis valves. Length, 3 mm.

Female: Like male except for sexual differences in head, (Fig. 8b), pilosity shorter on dorsum of thorax, abdominal lateral lines narrower. Length, 3 mm.

Distribution: KANSAS: Clark Co.; Liberal; Stafford Co. Salt Marsh. NEW MEXICO: 25 mi. west of Tularosa. TEXAS: Corpus Christi (holotype, allotype, and 15 paratypes); Galveston; Padre Island.

Holotype, male, and allotype, female: Corpus Christi, Texas, January 1, 1946 (R. H. Beamer), in the Snow Entomological Museum at the University of Kansas.

Flight records: December 12 and January 1 (southern Texas), June 22 (Kansas).

Nemotelus flavicornis Johnson

(Fig. 27)

Nemotelus flavicornis Johnson, 1894, Proc. Acad. Nat. Sci. Philadelphia, p. 272; Melander, 1903, Psyche, vol. 10, p. 191; Aldrich, 1905, Cat. N. Amer. Diptera, Sm. Inst., p. 190.

This species is closely related to *slossonae*. These two species are unique among the species of this subgenus in having largely

whitish abdomens in the males. The thorax of *flavicornis* has a greenish blue iridescence and the humeral calli are completely creamy white.

Male: Facial prominence black, shining, one third of width of eye. Antennae yellowish tan, terminal pseudosegment darker, flagellum black. Thorax shining black with bluish luster. Pubescence short, sparse. Lateral margins of mesonotum pale yellow forming broad lateral lines. Humeri entirely pale yellow. Halteres with knobs white. Fore and middle femora yellowish with brownish tinge, hind femora mostly yellow with medial black band; fore and middle tibiae yellowish, hind tibiae with basal half and apical tip yellow, apical half excepting tip, black; tarsi pale yellow. Wing vein R_4 absent. Abdomen pale yellow, fourth tergite with median black triangle, fifth tergite black basally. Genitalia small, widest toward apex, ventral bridge shallowly emarginate at apical margin; apical processes of gonocoxites short, more widely separated than their lengths (Fig. 27). Length, 3 mm.

Female: Unknown.

Distribution: FLORIDA: Key Largo, July 19, 1939 (R. H. Beamer). The only other locality record at present is the type locality in Jamaica.

Holotype, male: Kingston, Jamaica, in the Museum of Comparative Zoology at Harvard University.

Nemotelus slossonae Johnson

(Fig. 25)

Nemotelus slossonae Johnson, 1895, Proc. Acad. Nat. Sci. Philadelphia, p. 304; Melander, 1903, Psyche, vol. 10, p. 181; Johnson, 1913, Bull. Amer. Mus. Nat. Hist., vol. 32, p. 49.

This small species has a black thorax and mostly white abdomen in the male. The female has white lateral abdominal lines. It is closely related to *flavicornis*, another Floridian species, the genitalia of both being very similar.

Male: Facial prominence shining, less than one third of width of eye. Frontal spots creamy white. Antennae brown. Thorax shining black; pubescence on dorsum very sparse. Mesonotum with lateral edges pale yellow, forming broad lines from humeral calli to wing bases. Humeral calli creamy white except anterior corners which are brownish. Halteres with knobs white. Femora black except for pale yellow apices; fore tibiae yellow, slightly infuscated, middle and hind tibiae brownish black with pale yellow bases and apices; tarsi pale yellow. Wing vein R_4 absent. Abdomen mostly creamy white; first tergite with black spot immediately beneath

scutellum; fourth tergite with three indistinct brownish spots; fifth tergite with anterior half brownish black. Sternites mostly white with indistinct brownish blotches. In one specimen the fourth tergite has only one medial triangular spot. Genitalia very small, similar to that of *flavicornis*; apical prongs of dorsal process of aedeagus divergent, longer than the separation between them (Fig. 25). Length, 3 mm.

Female: Like male except for sexual difference in head, and in abdomen which is black with thin lateral pale yellow lines on margins of terga two to five. Length, 3.4 mm.

Distribution: FLORIDA: Big Pine Key; Fruitville; Homestead; Key West; Merritt Islands; Mims; Saddlebunch Keys; Tampa.

Holotype, male: Charlotte Harbor, Florida, in the Museum of Comparative Zoology at Harvard University. Allotype, female: Punta Gorda, Florida, Nov. 11, 1911, in the American Museum of Natural History, New York City.

Flight records: January 29, February 12, March 18, April 4, June 22, July 20, 25, August 11, December 29.

Nemotelus albinmarginatus James

(Figs. 5, 26)

Nemotelus albinmarginatus James, 1936, Bull. Brooklyn Ent. Soc., vol. 31, pp. 86, 87.

This species is easily distinguished from the similar *canadensis* by the creamy-white apices of the fifth and sixth abdominal terga and larger pale areas on the sides of the thorax and abdomen.

Male: Shining black with slight bluish iridescence. Facial prominence moderately long, about one third to one half width of eye viewed laterally; frontal spots contiguous, large, creamy white; antennae brownish black. Thorax densely pilose, hairs very long, white; suberect; mesonotal lateral margins broadly creamy white; humeral calli nearly entirely creamy white; supra-alar calli marked with creamy white; halteres with knobs white. Femora black with pale yellow apices; fore and middle tibiae yellow, hind tibiae yellow, each with transverse black mesal annulus; tarsi pale yellow, terminal segment slightly infuscated. Abdomen concolorous with thorax except the lateral margins of both terga and sterna (except the first segment) and apices of fifth and sixth terga and third, fourth, and fifth sterna which are creamy white. Gonostyli broad with distinct lobe on inner edge; emargination of ventral bridge of gonocoxites evenly rounded, moderately deep; penis valves narrow, pointed apically as seen from dorsal aspect (Fig. 26). Length, 5 mm.

Female: Like male except for shorter pilosity, especially on dorsum of thorax, and the usual sexual differences in head.

Distribution: CALIFORNIA: Benton, Mono Co.; Big Pine and Little Lake, Inyo Co.; Panocho Creek, Fresno Co.; Wood Lake, Tulare Co. IDAHO: Caldwell; Wilder. NEVADA: Valley Hot Spring, Douglas Co. OREGON: Burns. UTAH: Beaver; Delta; Duchesne; Farmington; Hayden; Hooper; Kingston; La Point; Myton; Ogden; Plain City; Riverdale. WASHINGTON: Walla Walla; Yakima. BRITISH COLUMBIA: Oliver.

Holotype, male: Kingston, Utah, June 19, 1935 (C. J. Sorenson), in the United States National Museum.

Flight records: March 24 (Fresno Co., California) to August 6 (British Columbia).

Nemotelus sabroskyi sp. nov.

(Fig. 28)

This coastal species has rather small frontal spots and pale yellowish buff halteres which distinguish it from the slightly larger but similar *communis*. The pile on the dorsum of the thorax is also much shorter.

Male: Body color shining black with slight bluish iridescence, more pronounced on face. Facial prominence moderately long (Fig. 1a); frontal spots pale yellow, small, contiguous; antennae brownish black. Thorax rather sparsely pilose, hairs white, moderately long near edges of dorsum, becoming very short and nearly absent mesally, extremely short on scutellum. Mesonotum with lateral margins narrowly yellowish tan. Each humeral callus with small yellowish spot above mesothoracic spiracle. Fore femora black with distal one third yellowish brown, second and third femora black with distal one fourth yellowish brown; fore and middle tibiae yellowish brown; hind tibiae with broad black band on middle portion, covering one third to one half of tibial length, basal and distal areas yellowish brown; tarsi yellowish tan. Halteres with knobs pale yellowish buff, paler beneath. Abdomen concolorous with thorax, pile very short, sparse. Gonostyli sharply pointed, expanded on inner edges before apices; aedeagus membranous, darker apically, penis with well-marked indentation at apex (Fig. 28). Length, 4 mm.

Female: Like male except for shorter pile and the usual sexual differences in head. Frontal spots usually very small, yellowish tan or sometimes yellow. Length, 4 mm.

Distribution: MARYLAND: Chesapeake Beach. NEW JERSEY: Atlantic City. NORTH CAROLINA: Southport.

Holotype, male U. S. N. M. no. 63263, and allotype, female: Southport, North Carolina, October 10, 1948 (C. W. Sabrosky) in the United States National Museum. Paratypes: 10 males, 14 females, same data.

Flight records: September 2 (New Jersey) to October 10 (North Carolina).

Nemotelus communis sp. nov.

(Figs. 6, 29)

Specimens of this species, usually determined as *canadensis*, differ from that species in lacking yellowish lateral margins on the third, fourth, and fifth abdominal terga, and in having a more tapering facial prominence. The pile on the dorsum of the thorax is finer and the black areas on the hind tibiae are much more extensive. This species resembles more closely *politus*, which occurs in much of its range of distribution. The humeral spot in *communis* is usually larger, covering half of each humeral callus, and the male genitalia differ considerably. In *politus* the ventral bridge is deeply emarginated apically and the aedeagus is short, the penis shorter than the penis valves. In *communis* the ventral bridge is not emarginate but has a double notch effect. The penis is equal in length to the penis valves (Figs. 16 and 29).

Male: Body color shining black with slight bluish iridescence more pronounced on dorsum of thorax. Facial prominence rather long and tapered (Fig. 6a) with two contiguous creamy white spots above antennae. Antennae brownish black. Thorax pilose on dorsum, the hairs rather evenly spaced, white, erect, their lengths about equal over entire dorsum. Humeral calli with large creamy white spot covering about half of dorsal surface of each. Lateral margins of mesonotum creamy white, moderately broad. Halteres with knobs white. Femora black with yellow apices; fore and middle tibiae yellow, hind tibiae mostly black with yellow bases and apices; tarsi pale yellow, the apical segments tinged with light brown. Abdomen entirely black with long white pile, sparser than on thorax. Genitalia large; ventral bridge of gonocoxites with an apparent double notch on posterior margin; gonostyli curved, with rounded apices; aedeagus membranous, the penis valves bent outward at apices; penis equal in length to penis valves; aedeagal apodeme short, directed dorsad (Fig. 29). Length, 4.5 mm.

Female: Like male except for shorter pile and the usual sexual differences in head (Fig. 6b). Length, 4.8 mm.

Distribution: ARIZONA: Apache Co.; Chiricahua Mountains; Faraway Ranch. COLORADO: Macedonia; Manzanola; Roggen; Sugar City; Vineland; Wray. IDAHO: Pine Lodge; Stone. ILLINOIS: Chicago. INDIANA: Lafayette. IOWA: Ocheyedon. KANSAS: Leavenworth Co.; Liberal; Meade Co.; Medicine Lodge; Menlo; Stafford Co. MINNESOTA: Big Stone Co. MONTANA: Hamilton. MICHIGAN: Midland Co. NEBRASKA: Morrill Co.; Willow Island, Dawson Co. NEW MEXICO: Albuquerque; Belen; Socorro. OREGON: Rest Lake. SOUTH DAKOTA: Aberdeen; Jefferson; Rapid City. UTAH: American Fork; Antelope; Bert; Blue Creek; Brigham; Clawson; Delta; Duchesne; Goshen; Huntsville; Lampo; La Point; Low; Lyndyl; Murray; Myton; Plain City; Promontory; Richfield; River-ton; Roosevelt; Salt Lake City; Santaquin; Springville; St. George; Syracuse; Tremonton; Tridell; Vernal. WYOMING: Teton Pass. MANITOBA: Baldur; Beulah; Red Deer River.

Holotype, male, and allotype, female: Duchesne, Utah, June 29, 1954, on goldenrod (Knowlton), in the Snow Entomological Museum at the University of Kansas. Paratypes: thirty males and thirty females, same data as holotype.

Flight records: June 6 (Utah) to September 15 (New Mexico).

Nemotelus beameri James

(Figs. 1, 32)

Nemotelus beameri James, 1933, Jour. Kansas Ent. Soc., vol. 6, p. 70.

The relatively long, tapering facial projection is distinctive in most individuals of this species, but in a few of the specimens available the projection is not noticeably different from that of some specimens of *nigrinus*. The large genitalia with membranous aedeagus and lanceolate penis are distinctive (Fig. 32).

Female: Body color shining black. Facial prominence long, its upper margin, viewed laterally, forming a continuous gentle sloping line with the vertex (Fig. 3b); frontal spots absent; antennae black. Thorax sparsely pilose, the hairs white and short, longer and more dense at lateral edges of mesonotum, very short on scutellum. Mesonotum with lateral margins pale yellow, resulting in a thin line on each side; humeral calli with small, pale yellow spot above each mesothoracic spiracle. Knobs of halteres white, slightly buff in some. Femora black with yellow apices; fore and middle tibiae yellow; hind tibiae mostly black with yellow bases and apices;

tarsi pale yellow. Abdomen concolorous with thorax, pile more sparse. Length, 4.5-5 mm.

Male: Like female except for sexual differences in head (Fig. 1a), dorsum of thorax with pilosity much longer, less sparse, but short on scutellum. Genitalia large; gonostyli long, rather straight; apical process of gonocoxites longer than gonostyli; ventral bridge of gonocoxites very shallowly emarginate; apodemes long, parallel; basal lamellae large, extending to near apices of apodemes. Aedeagus very long; penis valves slightly longer than penis, which is lanceolate and indented at apex. Length, 4.5-5 mm.

Distribution: ARIZONA: TUCSON. COLORADO: Boulder; Florissant; Glen Haven; Greeley. ILLINOIS: Chicago. IOWA: Dan Green's Stough, Clay Co.; Ocheyedon; Ruthven. KANSAS: Meade Co. MINNESOTA: LESUEUR Co. MONTANA: Big Timber; Drummond. NEBRASKA: Lakeside, Sheridan Co. NEVADA: Ely. NEW MEXICO: Sapelle. SOUTH DAKOTA: (no specific locality). UTAH: Duchesne; Greenville; Helper; Kanab; Manila; Springville. WYOMING: Lander; Lusk; Moran; Tie Siding.

Holotype, female: Northgate, Colorado, August 20, 1931, (R. H. Beamer) in the Snow Entomological Museum at the University of Kansas. Allotype, male (here designated): Drummond, Montana, August 11, 1931 (J. O. Nottingham), also in the Snow Entomological Museum.

Flight records: March 8 (Arizona) to September 12 (Minnesota).

Nemotelus picinus sp. nov.

(Fig. 30)

This species is distributed in the Great Lakes region west to Minnesota and Iowa, and is almost indistinguishable externally from *centralis*. The differences in male genitalia, as given in the discussion of that species, are so distinct that determination of the males is not difficult. Unfortunately, no adequate differences in the females have been found.

Male: Body color shining black (some individuals with slight bluish luster). Facial prominence as in *glaber*, pointed (Fig. 4a). Frontal spots absent (a few individuals with small yellow spots). Antennae brown (basal segments slightly orange brown in some individuals), small. Thorax with short pubescence on dorsum, longer near lateral margins, becoming absent mesally. Mesonotum with lateral margins narrowly yellow. Humeral calli with small yellow spot above each mesothoracic spiracle. Halteres with knobs

brown dorsally and apically. Femora black with yellow apices; fore tibiae yellowish brown, middle and hind tibiae brownish black; tarsi pale yellow. Abdomen concolorous with thorax. Genital capsule with rectangular shape as seen from dorsal aspect; gonostyli slightly curved, with subapical lobe on inner margin. Gonocoxal apodemes long, parallel; basal lamellae absent; penis valves longer than penis, truncated and wider at apices (Fig. 30). Length, 4 mm.

Female: Like male except for sexual differences in head. Length, 4 mm.

Distribution: ILLINOIS: Algonquin; Chicago; Monticello; Princeton. INDIANA: Lafayette. IOWA: Ames. MICHIGAN: Cheboygan Co.; Lenawee Co.; Vandalia. MINNESOTA: Minneapolis; St. Anthony Park; Wadena. WISCONSIN: Dane Co.; Madison; Wingra Lake. ONTARIO: Toronto. QUEBEC: Hemmingford.

Holotype, male: Chicago, Illinois, July 6, 1895 (Wheeler); allotype, female: Algonquin, Illinois, July 20, 1907 (Nasen), both in the collections of the Illinois Natural History Survey, Urbana, Illinois. Paratypes (ten males and five females): Ames, Iowa, July 10, 1951 (M. Cochran), July 12, 1947 and June 10, 1951 (J. Laffoon), Minneapolis, Minnesota, July 5, 1922 (A. Hertig), Wadena, Minnesota, July 4, 1922 (W. Hoffman), Dane County, Wisconsin, July 6, 1951, Princeton, Illinois, July 2, 1936 (Burks).

Flight records: June and July.

Nemotelus tenuistylus sp. nov.

(Fig. 31)

The broad lateral thoracic lines and nearly entirely yellow humeral calli are conspicuous characters which separate this species from all others with completely black abdomens. It is a widespread western species, its relationship to other species indefinite.

Male: Body color shining black with slight bluish iridescence. Facial prominence moderately long as in *communis* (Fig. 6a); frontal spots creamy white; antennae brownish black. Thorax with short, subappressed pile on dorsum, longer near lateral margins; mesonotum with lateral edges broadly yellow, the lateral line widest posteriorly; humeral calli nearly entirely pale yellow, except for anterior corner which is black. Halteres with knobs white. Fore femora with basal halves black, apical halves yellow, middle and hind femora with less yellow at apices; fore and middle tibiae yellow, hind tibiae with narrow black mesal bands; tarsi pale yellow. Abdomen concolorous with thorax, sparsely pilose. Gonostyli

nearly straight, long, at least distal half tapered; emargination of ventral bridge of gonocoxites shallow, V-shaped, acute; gonocoxal apodemes long; aedeagus long, narrow, penis valves sharply divergent at apices; prongs of dorsal process several times longer than their basal separation (Fig. 29). Length 3.4 mm.

Female: Like male except for sexual differences in head and shorter pilosity on dorsum of thorax. Length, 3.2 mm.

Distribution: CALIFORNIA: Needles. IDAHO: Nampa. KANSAS: Liberal; McPherson Co.; Meade Co. NEVADA: Carson City; Fallen. NEW MEXICO: Las Cruces. UTAH: Corinne; Garland; Grantsville; Randlett; St. George.

Holotype, male U. S. N. M. no. 63262: Las Cruces, New Mexico, June 16, 1917 (Aldrich); allotype, female: same locality, Sept. 25, 1895 (Cockerell), both in the United States National Museum.

Flight records: June 15 (Utah) to September 25 (New Mexico).

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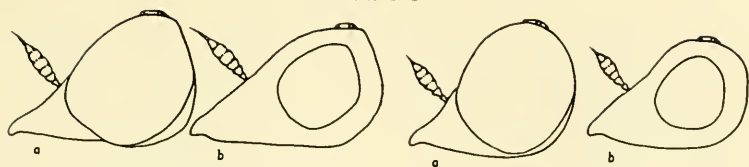
1903. A Review of the North American Species of *Nemotelus*. Psyche, vol. 10, pp. 171-183.

FIGURES 1-9

FIGS. 1-8. Lateral aspects of heads of certain species of *Melanonemotelus*;
a, male, b, female.

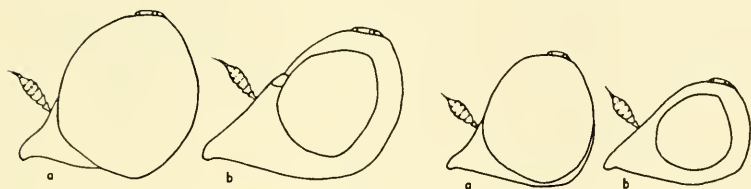
FIG. 9. *Melanonemotelus* wing.

FIGS. 1-9



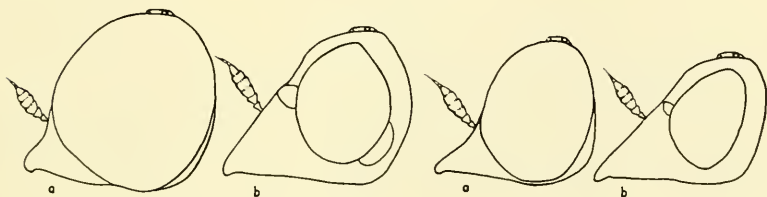
1. *beameri*

nigrinus



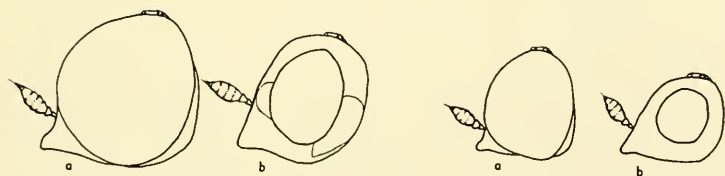
3. *canadensis*

4. *glaber*



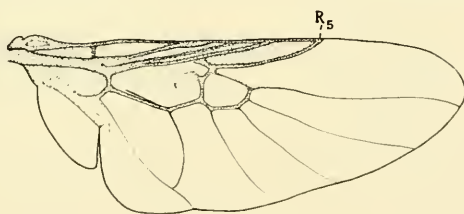
5. *albimarginatus*

6. *communis*



7. *lambda*

8. *melanderi*



9

FIGURES 10-14

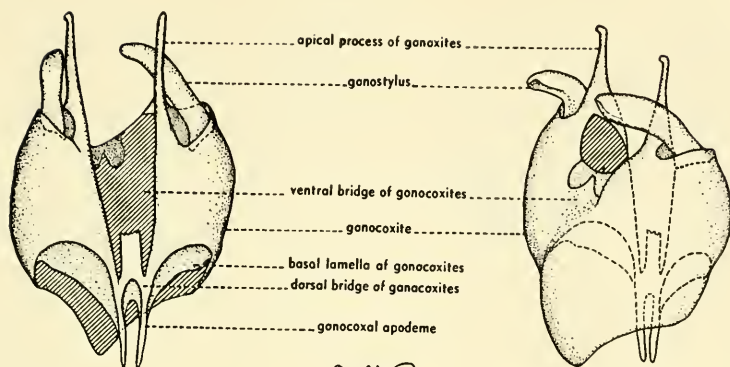
FIG. 10. Laterodorsal aspect of genital capsule of male.

FIG. 11. Lateroventral aspect of genital capsule of male.

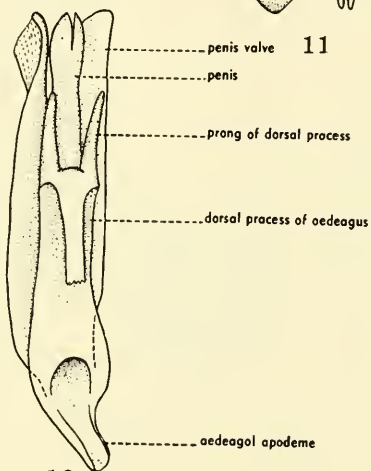
FIG. 12. Laterodorsal aspect of aedeagus.

FIGS. 13 and 14. a. Dorsal aspect of genital capsule. b. Dorsal aspect of aedeagus. c. Lateral aspect of gonostylus. d. Lateral aspect of apex of genital capsule, showing apical process of gonocoxites.

FIGS. 10-14

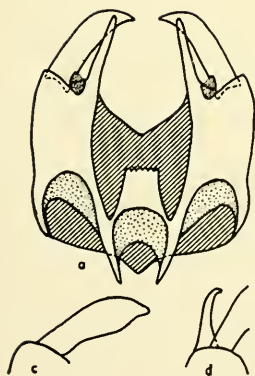


10

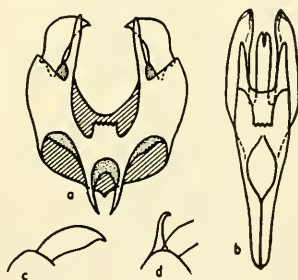


11

12



13. *nigrinus*

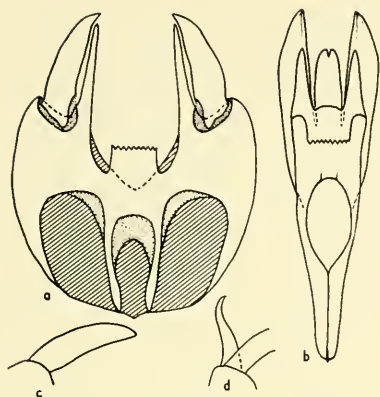


14. *glaber*

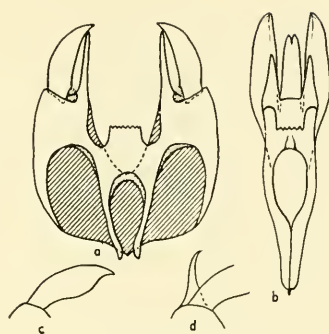
FIGURES 15-20

FIGS. 15-20. a. Dorsal aspect of genital capsule of male. b. Dorsal aspect of aedeagus. c. Lateral aspect of gonostylus. d. Lateral aspect of apex of genital capsule, showing apical process of gonocoxites.

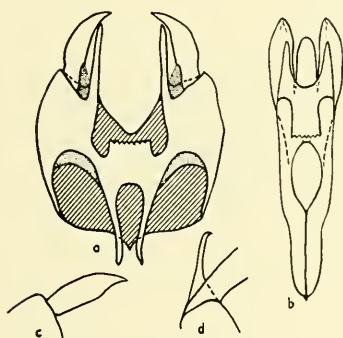
FIGS. 15-20



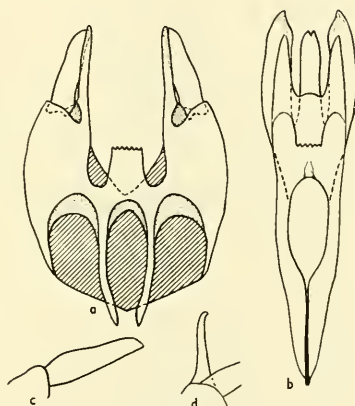
15. canadensis



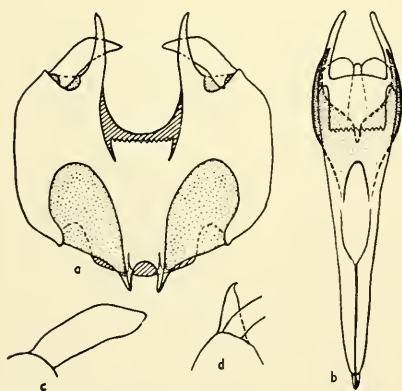
16. politus



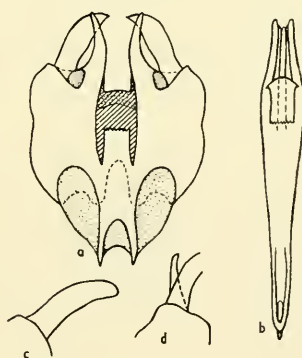
17. tristis



18. arator



19. jamesi

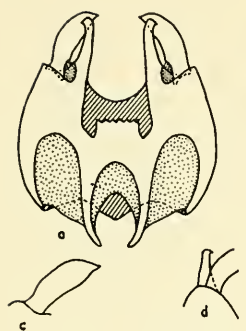


20. variabilis

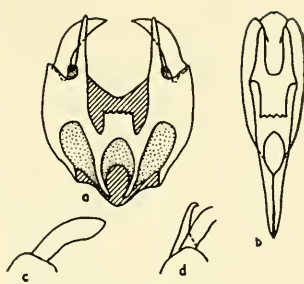
FIGURES 21-27

FIGS. 21-27. a. Dorsal aspect of genital capsule of male. b. Dorsal aspect of aedeagus. c. Lateral aspect of gonostylus. d. Lateral aspect of apex of genital capsule, showing apical process of gonocoxites.

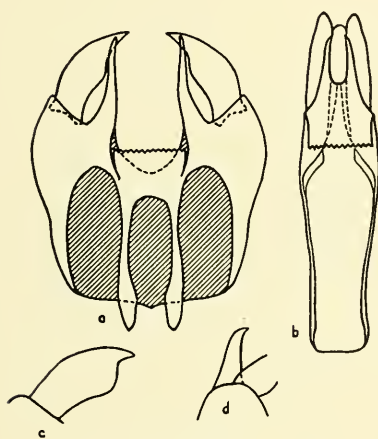
FIGS. 21-27



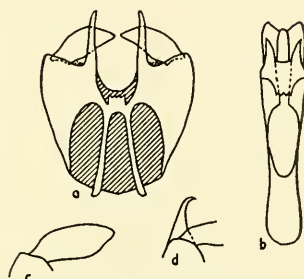
21. *centralis*



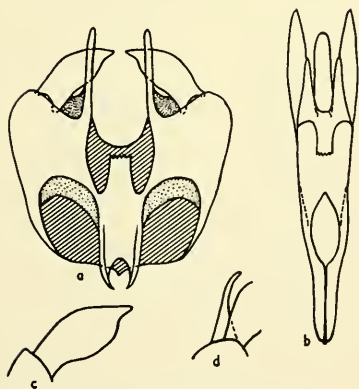
22. *melanderi*



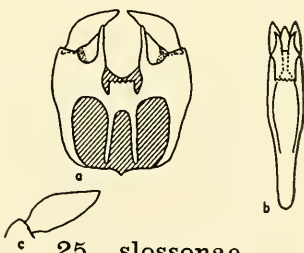
24. *lambda*



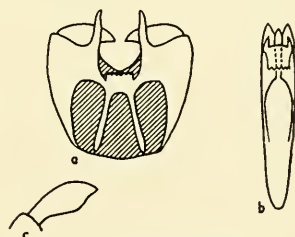
23. *halophilus*



26. *albimarginatus*



25. *slossonae*

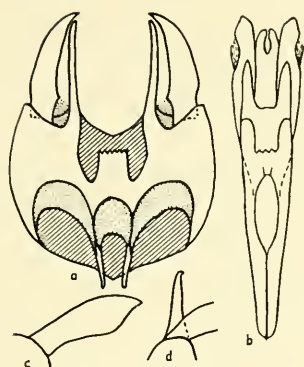


27. *flavicornis*

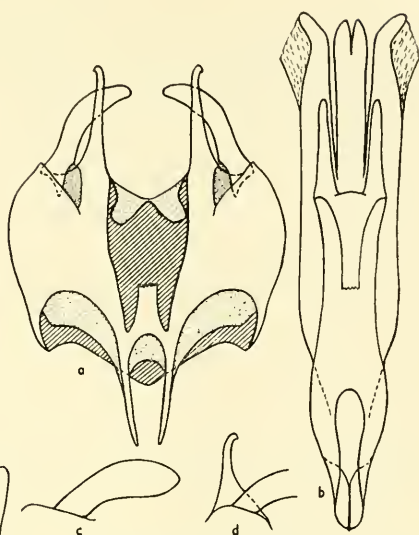
FIGURES 28-32

FIGS. 28-32. a. Dorsal aspect of genital capsule of male. b. Dorsal aspect of aedeagus. c. Lateral aspect of gonostylus. d. Lateral aspect of apex of genital capsule, showing apical process of gonocoxites.

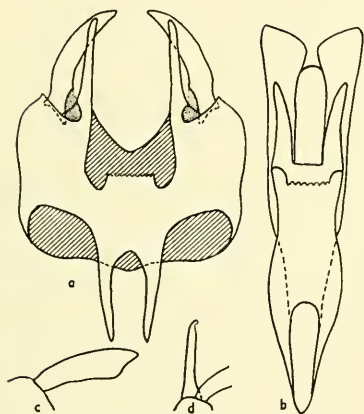
FIGS. 28-32



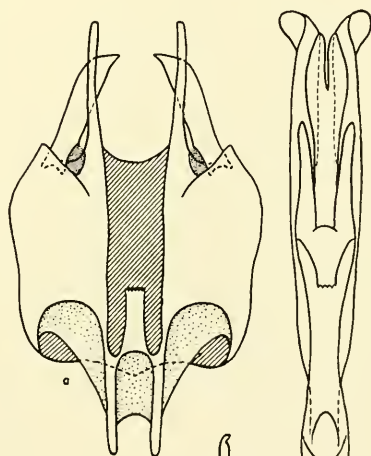
28. *sabroskyi*



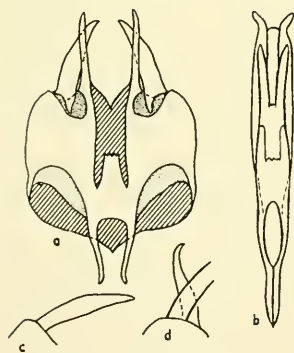
29. *communis*



30. *picinus*



32. *beameri*



31. *tenuistylus*

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[No. 20

Two New Fossil Plants from the Pliocene of Northwestern Texas *

BY

A. BYRON LEONARD **

ABSTRACT. Two new fossil plants, *Biorbia papillosa* and *Panicum eliasi*, are described from the Ogallala Formation of Lubbock County, northwestern Texas.

Investigations of Cenozoic stratigraphy and paleontology in the Texas High Plains, now in progress by John C. Frye and myself under the auspices of the Bureau of Economic Geology of the University of Texas, have resulted in the discovery of several outcrops of Pliocene (Ogallala formation) deposits containing assemblages of fossil seeds. One of the most prolific of these exposures is situated on the prominent Pliocene escarpment a few miles west of the town of Post, Garza County, Texas. Included in the assemblage are an undescribed species of *Biorbia* (Boraginaceae) represented by a large series of nutlets of this plant and an undescribed species of *Panicum* (tribe Paniceae, millet grasses) represented by the fertile glumes that cover the caryopsis or grain. The starchy caryopsis or grain, and the chafflike infertile glumes are invariably wanting in these seeds, but the delicate pericarp may sometimes be preserved. Fortunately, both the nutlets of borages and the fertile glumes (lemma and palea) of grasses bear some of the most diagnostic characters of these plants, so that accurate determinations are possible from these parts alone.

The seeds described here occur in partly cemented sands and gravels; the cementing substance is calcium carbonate for the

* Published with the permission of the Director, The University of Texas Bureau of Economic Geology.

** Department of Zoology, University of Kansas, Lawrence, Kansas.

most part, but the seeds are opalized, which permits their being cleaned by dissolving the calcite with dilute acid, thus freeing the seeds of adhering sand and gravel. Seeds are collected by handpicking from the exposed face of the outcrop; no more productive method of collecting seeds from these sediments has been devised, because of the cementation present.

These and other fossil seeds from the Pliocene of the Great Plains are catalogued with the collections of Cenozoic mollusks maintained at the Museum of Natural History of the University of Kansas.

SUBCLASS DICOTYLEDONAE

Series GAMETOPETALEAE

FAMILY BORAGINACEAE

Genus *BIORBIA* Elias, 1932

Biorbia fossilia * is the name applied to the nutlets of the boraginaceous plant abundantly represented in late Tertiary sediments of the Great Plains by these well-preserved fruits. Since there exists in the literature some confusion concerning the appropriate name of the plant that produced these nutlets, a review of the nomenclature seems in order.

The genus *Biorbia* was erected by Elias (1932, p. 350) to receive *Biorbia rugosa* (Berry) Elias, originally described by Berry (1928, art. 13, p. 1) as *Lithospermum fossilium* var. *rugosum*. At the time, Berry had before him a collection of Tertiary seeds collected by John B. Hatcher; these Berry described as three varieties of a single new species, viz., *Lithospermum fossilium* var. *rugosum*, *L. f.* var. *glabrum*, and *L. f.* *aristatum*. Later in the same year, Brooks (1928) described the same nutlets as *Celtis microendocarpica*, but since Berry's name has date priority, Brooks' name has no real bearing on the history of the name of the plant in question. In 1931 Elias, realizing that Berry's material consisted of fossil seeds not properly assigned to the genus *Lithospermum*, and recognizing that Berry's *L. f.* *rugosum* was actually a borage, while the other two varieties of *L. fossilium* were grasses, invented the new name combination *Biorbia rugosa* for the boraginaceous plant; *L. f.* *glabrum* and *L. f.* *aristatum* were assigned to a new genus *Berrichloa*. These were *nomina nuda* since they were not accompanied by descriptions or figures. The next year, however, Elias (1932, p. 350) validated the name *Biorbia rugosa* (Berry) by publishing an

* Prof. G. Ruggieri, University of Palermo, has called to my attention that the correct name combination is *Biorbia fossilis*.

adequate description, accompanied by figures. Cockerell (1933, p. 15), noting Elias' use of the name combination *Biorbia rugosa*, called attention to the fact that there was no justification in the suppression of the species name *L. fossilium*, and expressed the view that the correct name combination was *Biorbia fossilia* (Berry), on the grounds that the "first and most abundant variety . . . should be considered the typical form of the species" (Art. 63, 70, Int. Code Bot. Nomen.). The confusion was compounded by Elias (1942, p. 106), who used the name combination *Biorbia fossilia* (Berry) Elias, when it is obvious that Cockerell is the authority for the new combination. There seems no doubt that all these authors were writing of the nutlets of the same plant, so that the correct name of the species is *Biorbia fossilia* (Berry) Cockerell.

The history of the name, *Biorbia fossilia* (Berry) Cockerell may be summarized as follows:

Lithospermum fossilium var. *rugosum* Berry, 1932, Proc. U. S. Nat. Mus., vol. 73, art. 13, p. 1, Pl. 1, Figs. 1-10, May 1.

Celtis microendocarpica Brooks, 1928, Annals Carnegie Mus., vol. 18, p. 297, Pl. 18, Fig. 1, June 1.

Biorbia rugosa (Berry) Elias, 1931, State Geol. Surv. Kansas, Bull. 18, vol. 32, no. 7, p. 150, April 1. (*nomen nudum*)

Biorbia rugosa (Berry) Elias, 1932, Kansas Univ. Sci. Bull., vol. 20, p. 350, Pl. 29, Figs. 2a, 2b, 2c, 3, May 15. New name combination.

Biorbia fossilia (Berry) Cockerell, 1933, Torreya, vol. 33, no. 1, p. 15. Jan.-Feb. New name combination.

Biorbia fossilia (Berry) Elias, 1942, Geol. Soc. America, sp. papers, no. 41, p. 106, Pl. 15, Fig. 12. November 25. Incorrect authority for name combination.

The genus *Biorbia* was described as follows (Elias, 1932, p. 350): "Only nutlets known. Nutlets keeled, asymmetrically inflated, being more convex on the dorsal side. Surface rugose covered with ridges arranged in honeycomblike net. Dorsal keel turns to right or to left, spoiling the apparent bilateral symmetry of the nutlets. Probably four nutlets, two right and two left ones, constituted a complete fruit. Scar of attachment round, comparatively small and elevated, consists of double ring and an elaiosome in the center. Distinct canal in the ventral part of the scar."

"Genotype: *Lithospermum fossilium* var. *rugosum* Berry. U. S. National Museum."

Biorbia papillosa, sp. nov.

(Plate I, Figures 1, 2, 3)

Types.—Holotype, catalogue number 9917; 160 paratypic examples from the type locality, catalogue number 9918. Collected by A. B. Leonard and John C. Frye, June 30, 1955; original number, A. B. Leonard, 742. Five paratypic examples, catalogue number 9983, from Ogallala formation in Tierra Blanca Canyon, near dam of Buffalo Lake, Lubbock County, Texas. Collected by John C. Frye and A. B. Leonard, July 6, 1955; original number, A. B. Leonard, 765.

Type locality.—Partly cemented sand and gravel at the rim of the escarpment produced by resistant Pliocene deposits, 3.8 mi. west of intersection of U. S. Highway 380 and U. S. Highway 84 near the center of the town of Post, Garza County, Texas.

Diagnosis.—A small nutlet of a boraginaceous plant; nutlet generally ovoid in shape; base inflated, tapering toward pointed apex, but also compressed laterally; scar of attachment circular, rim elevated; surface sculpture densely papillose; similar in general form to the nutlets of *Biorbia fossilia* (Berry) Cockerell, but differing in: smaller size (total length less than 2.0 mm), densely papillose rather than heavy reticulate surface sculpture, and in details of scar of attachment.

Description of holotype.—Nutlet small, total length 1.7 mm., transverse diameter, 1.3 mm., vertical diameter, 1.3 mm.; ovoid in shape, swollen near base, tapering toward cuspidate apex, but also compressed; ventral, bladelike ridge, arising from base of style at anterior rim of scar of attachment, extending forward in midline over apex, thence backward along mid-dorsal axis of nutlet for a short distance before extending diagonally to the left, over side of the nutlet to reach scar of attachment; surface sculpture of closely spaced, conical, papillose excrescences, varying in height from 0.2 to 0.3 mm.; in a few places along side of the nutlet, the papillae fused to form short ridges; scar of attachment circular in outline, depressed strongly in center, within outer rim a parallel groove, followed medially by a parallel row of six low, rounded papillae or bosses; in center of scar of attachment a small cylindrical elevation (elaiosome ?) rising slightly above outer rim of scar; the style, situated on anterior rim of scar at point of origin of keel, elevated

well above rim of scar, spatulate, possessing a large median vein and two smaller, parallel veins laterally.

Variations and comparisons.—Size varies little, the largest specimens being slightly under 2.0 mm. in length. The ventral keeled ridge, after rising over apex of nutlet, may turn either to the left, as in the holotype, or to the right. This seeming random division of the seeds into two groups on the basis of the course of the characteristic keeled ridge is similar to the condition in *Biorbia fossilia*. On certain paratypic individuals, the coalescence of papillae into ridges has resulted in an anastomosing, reticulate pattern, like that typically found on *B. fossilia*, except that the intervening spaces are invariably papillose. No smooth seeds, like those commonly found in large series of *B. fossilia*, have been observed among *B. papillosa*. The scar of attachment of *B. papillosa* differs from that on the nutlet of *B. fossilia* in the number of bosses on the inner circlet within the depressed central area of the scar; *B. fossilia* commonly bears twelve or more of these knoblike elevations. In general, *B. papillosa* is distinguished most readily from *B. fossilia* by its smaller size, its papillose rather than reticulate surface sculpture, and its more cuspidate apex. The ventral ridge on the nutlets of *B. papillosa* invariably arises from the base of the style on the scar of attachment; this is not always the case among nutlets of *B. fossilia*.

Remarks.—In the same assemblage with *Biorbia papillosa* were seeds of the hackberry, *Celtis willistoni* Cockerell, and four grasses, including the species of *Panicum* described below, a single example of a seemingly undescribed *Panicum* related to the living *Panicum fasciculatum*, *Berriehloa tuberculata* Elias, and fragments of hulls of an undescribed species of *Stipidium*.

It is difficult to make specific stratigraphic assessment of the sediments bearing this assemblage of seeds, beyond the reasonable judgment that the outcrop should be assigned to the equivalent of the Ash Hollow member of the Ogallala formation. *Berriehloa tuberculata* is, so far as known, restricted to the Ash Hollow; all previous records of *Panicum* are from this stratigraphic unit, and all previous records of *Biorbia* are found within the span of Ash Hollow deposition. *Celtis willistoni* has a vertical range that precludes its having any value for precise stratigraphic placement of these outcrops.

SUBCLASS MONOCOTYLEDONAE

Order GLUMIFLORAE

FAMILY GRAMINEAE

SUBFAMILY PANICOIDEAE—TRIBE PANICEAE, The Millet Grasses

Genus *Panicum* Linnaeus

As far as the fruits are concerned, the genus *Panicum* Linnaeus may be characterized as follows: glumes unequal, the first often minute, the second subequal to the sterile lemma which often encloses a hyaline palea and rarely a staminate; fertile lemma and palea chartaceous-indurated, veins obsolete, the margins of the lemma inrolled; grain (starchy caryopsis) free within the rigid, firmly closed lemma and palea.

Panicum eliasi, sp. nov.

(Plate I, Figures 7, 8, 9, 16)

Types.—Holotype, catalogue number 9975; 15 paratypic examples, catalogue number 9976, from type locality. Collected 30 June 1955 by A. B. Leonard and John C. Frye; original number, A. B. Leonard, 752. Twenty-nine paratypic examples, catalogue number 9978, from Ogallala deposits exposed along Acuff Road, in north valley wall of North Fork of Double Mountain Fork of Brazos River, 5 mi. S Acuff, Lubbock County, Texas. Collected by A. B. Leonard and John C. Frye, 6 July 1955; original number, A. B. Leonard, 765.

Type locality.—Partly cemented sand and gravel at the rim of the Pliocene escarpment, 3.8 mi. W intersection U. S. Highway 380 and U. S. Highway 84 near center of the town of Post, Garza County, Texas.

Diagnosis.—A small seed of a panic or millet grass, about 2.5 mm., depressed ovoid in shape, swollen posteriorly, narrowing anteriorly to acuminate, produced apex; consisting of the fertile glumes; lemma enclosing palea, but the latter broadly exposed; surface sculpture of wrinkled transverse minute ridges, those on palea superimposed on minute longitudinal ridges; generally similar to *Panicum elegans* Elias, but differing in: size more variable, hull more depressed, apex more sharply acuminate, and surface transversely wrinkled, rather than smooth and glossy.

Description of holotype.—A small seed of a panic grass, represented by the fertile glumes; total length 2.4 mm., transverse diameter, 1.7 mm., vertical diameter, 1.4 mm.; depressed ovoid in

shape, greatest diameter (both vertical and transverse) slightly posterior to center of longitudinal axis, narrowing slowly to acuminate, produced apex; apex acute, bent slightly downward, consisting of central cylindrical spikelike projection and two smaller, lateral flanking ridges; inflated lemma enclosing palea, but latter broadly exposed; palea less inflated than lemma, greatest exposed diameter, 1.4 mm.; palea excavated anteriorly, especially just below reflexed apex, forming pitlike depression; surface sculpture of lemma wrinkled, transverse ridges, about 20 in a distance of 1 mm.; sculpture of palea similar but finer in texture, and superimposed upon minute longitudinal ridges; scar of attachment (not well preserved) compressed ovoid, 1.4 mm. in transverse diameter, the lesser diameter about one-third as great; surface impressed, pitted, style (?) on dorsal rim.

Variations and comparisons.—Size is variable, the largest specimens being slightly over three millimeters long, but otherwise observed characters are remarkably constant. *Panicum eliasi* differs from *P. fasciculatum* var. *reticulatum* (Torrey) Beal, a panic grass living in western Texas and widely dispersed elsewhere, in being less elongate and less conspicuously sculptured; *P. eliasi* is similar in size and shape to *P. schribernerianum* Nash, another panic grass living in the Great Plains, but differs in: acute rather than blunt apex, and in transverse rather than longitudinally arranged ridges.

Panicum eliasi is named in honor of Dr. Maxim K. Elias, noted among his many accomplishments for his pioneering (1932) and monographic studies (1942) of the floras of the Tertiary deposits of the Great Plains.

Remarks.—This is the second species of *Panicum* to be recognized in Tertiary deposits of the Great Plains, and represents the Geminata group, as evidenced by the sculptured surface of the fertile glumes. *P. elegans* is found in the upper part of Ash Hollow deposits as the Ogallala formation is understood elsewhere, but Elias (1942) has described a variety of *P. elegans* which occurs low in the Ash Hollow member in the lowest part of the *Biorbia fossilia* zone. Since the genus is known to occur throughout the Ash Hollow, the occurrence of *P. eliasi* throws no light on the precise stratigraphic placement of the beds, but it may be assumed that they occur within the equivalent of the Ash Hollow.

At the type locality, *Panicum eliasi* occurs with the assemblage of fossil seeds listed above; at the Acuff Road exposure, no other seeds were found with it.

It has generally been assumed (and often informally stated) that fossil seeds are rare or absent in Pliocene sediments south of west central Kansas. Indications from the collections made during a rapid reconnaissance of Cenozoic deposits in the Texas High Plains serve to dispel this erroneous impression, although it is possible that the rich prairie floras so characteristic of more northern portions of Pliocene deposits in the Great Plains (Frye and Leonard, 1956) may be less well represented. It is worthy of note, however, that the typology of the floral assemblage at the Post locality is similar to many assemblages found in northwestern Kansas (Frye and Leonard, 1956), and indicates that the southern High Plains in middle Pliocene time supported a mixed prairie vegetation, although individual species differ in certain cases.

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EXPLANATION OF FIGURES, PLATE I

FIGURES 1, 2, 3. Holotype of *Biorbia papillosa*, catalogue number 9917, from partly cemented sand and gravel in the Pliocene escarpment, 3.8 mi. W junction U. S. Highway 84 and U. S. Highway 380 in Post, Garza County, Texas. Lateral, ventral and dorsal views, respectively. Enlarged 10 times.

FIGURES 4, 5, 6. *Biorbia fossilia* (Berry) Cockerell, catalogue number 9648, from Ash Hollow deposits in NW $\frac{1}{4}$ NW $\frac{1}{4}$ Sec. 11, T. 3 S, R. 33 W, Rawlins County, Kansas. Lateral, ventral and dorsal views of three different nutlets. Enlarged 10 times.

FIGURES 7, 8, 9. Holotype of *Panicum eliasi*, catalogue number 9975, from partly cemented sand and gravel in the Pliocene escarpment, 3.8 mi. W junction U. S. Highway 84 and U. S. Highway 380 in Post, Garza County, Texas. Lateral, ventral and dorsal views, respectively. Enlarged 10 times.

FIGURES 10, 11, 12. *Panicum elegans* Elias, catalogue number 9639, from Ash Hollow deposits, center W line, SW $\frac{1}{4}$ Sec. 4, T. 4 S, R. 34 W, Rawlins County, Kansas. Lateral, ventral and dorsal views, respectively. Enlarged 10 times.

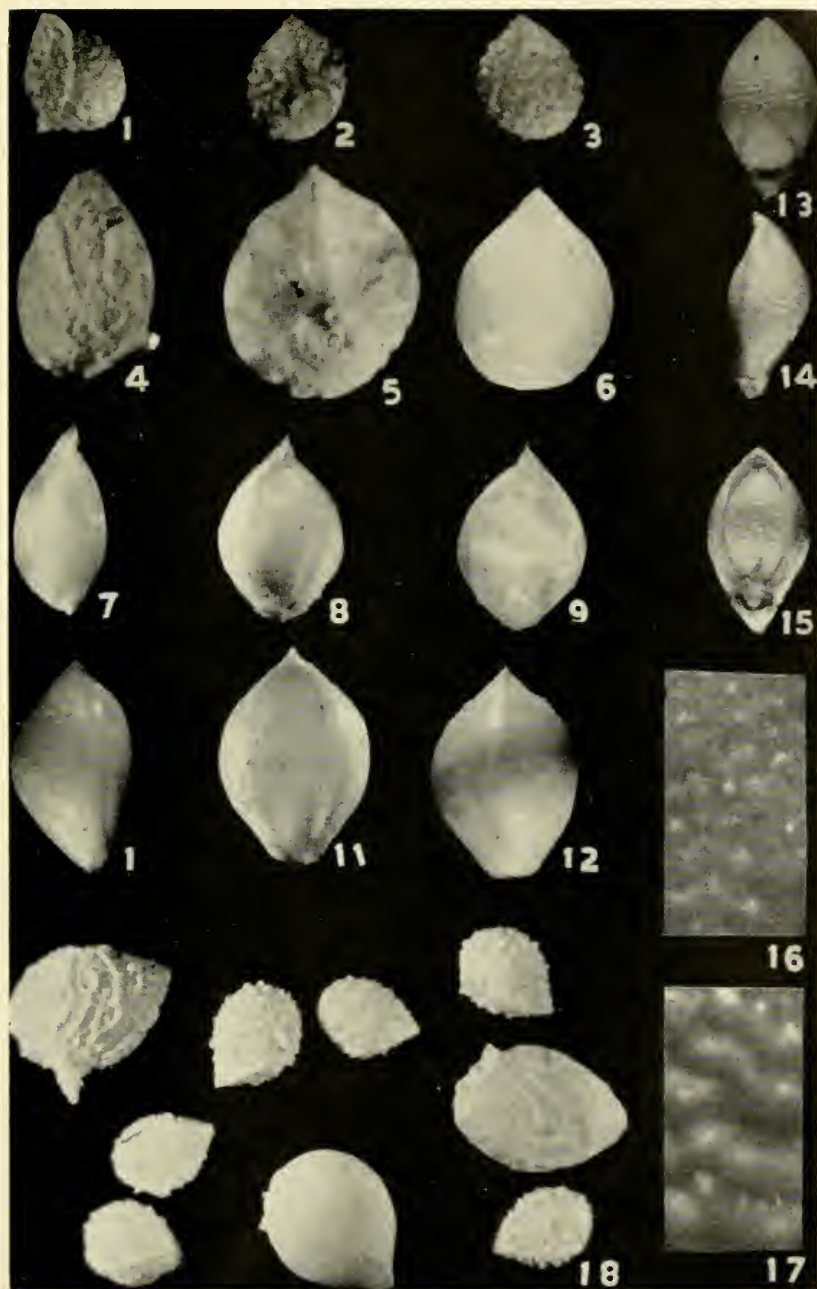
FIGURES 13, 14, 15. *Panicum fasciculatum* var. *reticulatum* (Torrey) Beal, catalogue number 9977, collected living 20 mi. S United States Conservation Service Nursery, San Antonio, Texas. Dorsal, lateral and ventral views, respectively. Enlarged 10 times. Courtesy of the Botany Department, The University of Kansas.

FIGURE 16. Detail of surface sculpture of holotype of *Panicum eliasi*, enlarged 120 times.

FIGURE 17. Detail of sculpture of *Panicum fasciculatum* var. *reticulatum* enlarged 120 times.

FIGURE 18. Paratypes of *Biorbia papillosa* with *B. fossilia*. Enlarged approximately 8 times.

PLATE I.



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[No. 21

Anatomical Findings at Autopsy Immediately Following Hanging

BY

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EDWIN C. GALBREATH *

ABSTRACT. Thirty-five minutes after hanging the head and neck were flushed with citrated Ringer's via both common carotids. This was followed with neutral 10 percent formalin. Examination of the remainder of the body was performed immediately without fixation. The anterior atlanto-occipital membrane and associated ligaments were ruptured as was the posterior atlanto-epistrophic membrane and ligaments. Associated vertebral musculature showed hemorrhagic areas. There was no evidence of any fractures in the cervical vertebrae. The odontoid process and associated ligaments were intact. Gross-examination of all major blood vessels, meninges, brain, and spinal cord showed no significant deviation from normal. There was evidence of petechial hemorrhages bilateral in the intermediate gray matter of the second cervical segment; no other histologic changes were noted on preliminary examination.

It was interesting to note that the pituitary gland was twice the normal size. Death apparently occurred from suffocation within thirteen minutes.

Anatomical findings immediately following hanging do not indicate sufficient structural damage to account for the death of the individual. We had a unique opportunity to do a complete dissection immediately after death from hanging; the results are reported here.

Through prearranged agreements with the condemned man, permission was granted to dissect the body as soon as possible after death. Within 35 minutes after the man was pronounced dead the head and neck were perfused through the common carotids with citrated Ringer's solution, followed by 10 percent neutral formalin. The brain was removed immediately following this procedure. It was well hardened in situ. The spinal cord was fixed by injecting 10 percent neutral formalin into the spinal canal with a 50 cc hand

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syringe. The cord was removed 10 hours later by a complete laminectomy.

Careful inspection showed no indication of hemorrhage or large clot. If there had been damage to the blood vessels to the extent that hemorrhages had occurred, this would not have been obscured by the flushing of the vessels.

All coverings of the brain and upper cord were intact. No major or minor cerebral blood vessel showed damage. If there was hemorrhage within the cranial cavity or brain we have been unable to detect it. Certainly no significant gross structural deviation could be detected.

Reports on the cause of death from hanging frequently state "broken neck" or "fractured cervical vertebrae." "Broken neck" is hard to define; clinically, it involves the crushing or fracture of vertebrae. In this case we cannot use the term "broken neck." However, we found that the anterior portion of the atlanto-occipital membrane and its associated ligaments were ruptured and torn slightly and, posteriorly, the atlanto-epistrophic membrane and ligaments were also torn. Hemorrhagic areas occurred in the intimately associated vertebral musculature. The odontoid process with its ligaments was intact.

The central nervous system showed little damage. A few petechial hemorrhages were present in the intermediate gray at the level of the second cervical segment. No other areas of the central nervous system showed signs of damage which are referable to the hanging. The pituitary was about twice its normal size. Blood channels through it appeared unusually large.

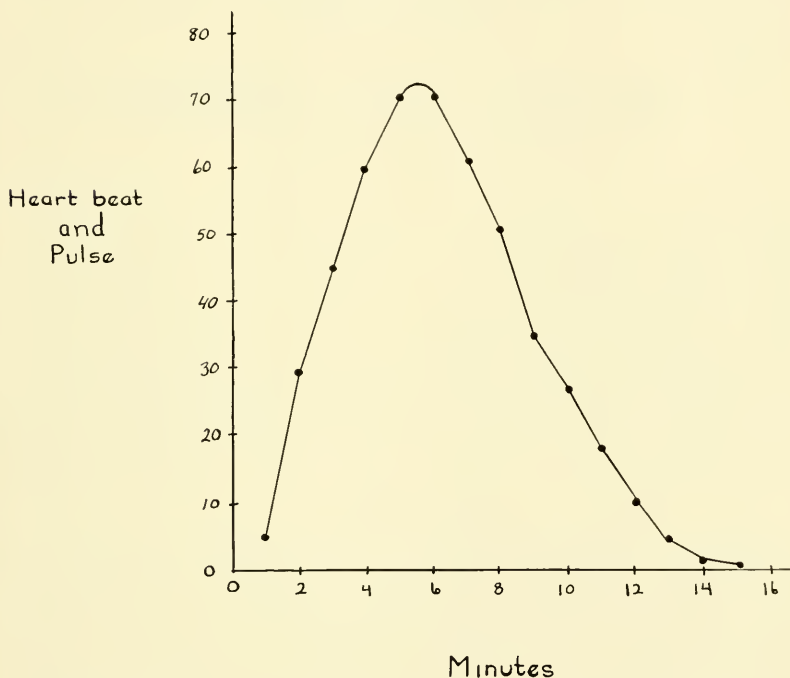
In this individual there was scattered chromatolysis throughout the cord; this was most marked in the lumbar and sacral areas. Marked ependymal hyperplasia was pronounced from the mid-thoracic area to the lower sacral. The ventral white commissure was displaced. However, no neurological signs were mentioned in his medical record. Scattered perivascular demyelination was found in the cerebral white matter in the few areas studied. How extensive this was is yet to be determined. None of the above changes could be attributed to the hanging.

The cortices of both cerebrum and cerebellum appeared normal. We have not yet investigated the medulla, pons, midbrain and thalamus.

The cause of death could not be determined. It is suggested that suffocation probably was the reason.

Legally, hanging is classified as traumatic asphyxia due to strangulation. The lumen of the upper portion of the larynx is effectually occluded by the direct pressure of the ligature which forces the base of the tongue upward and backward and depresses the epiglottis over the laryngeal opening. The compression applied to the throat from front to back and from the sides affects the superior laryngeal nerves, the vagus, the carotid arteries and the jugular veins, causing shock and direct disturbances to the cerebral circulation.

FIGURE 1.



The chart is a composite compiled from 12 case histories scattered in the literature, chiefly from E. Kalle, and indicates the sequence of events related to heart rate and pulse rate. The attending physician's report follows very closely the sequence of events indicated in the accompanying chart. Zero minutes corresponds to springing of the trap. We can only speculate as to the physiology involved.

Probably the traumatic irritation of the vagus and carotid body and sinus and the sudden shock and immediate closure of the laryngeal opening all contribute to this early low heart rate, if not its complete stoppage. In some instances the heart rate goes to 150 or higher in the 4 to 7 minute interval. The average time of death in these cases was roughly 13 minutes and 30 seconds. The increase of heart rate may be accounted for by the thoraco-lumbar activation with excessive adrenalin. Spasms may or may not occur. Gasping does not occur.

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[No. 22

A Statistical Method for Evaluating Systematic Relationships¹

BY

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ABSTRACT. Starting with correlation coefficients (based on numerous characters) among species of a systematic unit, the authors developed a method for grouping species, and regrouping the resultant assemblages, to form a classificatory hierarchy most easily expressed as a treelike diagram of relationships. The details of the method are described, using as an example a group of bees. The resulting classification was similar to that previously established by classical systematic methods, although some taxonomic changes were made in view of the new light thrown on relationships. The method is time consuming, although practical in isolated cases, with punched-card machines such as were used; it becomes generally practical with increasingly widely available digital computers.

INTRODUCTION

The purpose of the study reported here was to develop a quantitative index of relationship between any two species of a higher systematic unit, as well as to exploit such indices of association in the establishment of a satisfactory hierarchy. The authors became interested in the development of such a method when they attempted to find a technique for classifying organisms that was free from the subjectivity inherent in customary taxonomic procedure.

1. Contribution number 945 from the Department of Entomology, University of Kansas.

2. We wish to acknowledge the constructive criticism received in connection with this and related work from the following individuals who kindly gave their time to read and comment upon the manuscript: Paul R. Ehrlich, University of Kansas; Raymond B. Cattell, University of Illinois; Alfred E. Emerson, University of Chicago; Warwick E. Kerr, Universidade de São Paulo; Ernst Mayr, Harvard University; Louis L. McQuitty, Michigan State University; G. G. Simpson, American Museum of Natural History; Peter C. Silvester-Bradley, University of Kansas and University of Sheffield; and Paulo E. Vanzolini, Departamento de Zoologia, Secretaria de Agricultura, São Paulo. These persons, however, are not responsible for the opinions which we have expressed.

Acknowledgment is also due to the University of Kansas General Research Fund for assistance.

The systematic group chosen as a test of the feasibility of this undertaking was one consisting of 97 species of solitary bees in the family Megachilidae. This choice was made because one of us (C. D. M.) has made recent systematic studies of these insects, so that conclusions as to the relationships obtained by the usual systematic procedure could be compared with the results of the new method.

The findings of our study as well as the philosophical bases of our attempts at quantifying systematic relationships have been reported elsewhere (Michener and Sokal, 1957). In this paper we propose to describe in some detail the actual method employed, as well as our reasons for adopting it and for rejecting several alternate procedures. It is our intention to illustrate the procedures in sufficient detail so that persons with a limited knowledge of statistical methods will be able to follow our method. We expect our system to be applicable to most organisms, provided they exhibit a variety of characters, and the account to follow is consequently phrased in general terms. However, our practical illustrations are based on the bee group cited above in order to provide the reader with concrete examples.

A quantitative method of finding the relationship between two species must be based on a number of taxonomic characters in a manner similar to the traditional systematic approach. However, whereas the latter technique generally uses few characters and weights these quite unequally and subjectively, the former method employs numerous but unweighted characters. Our reasons for not weighting characters have been detailed in the companion paper (Michener and Sokal, 1957). In the absence of an objective criterion of character weight it seems best to rely on a large number of equally weighted characters. In our bee study we employed 122 characters per species; however, we feel significant results may be obtained from as few as 60 characters.

Our use of the word "character" will require some elaboration. In its commonest taxonomic usage, a character is any feature of one kind of organism that differentiates it from another kind. Thus the red abdomen of one bee is a character distinguishing it from another bee with the abdomen black. In this paper we use the word in a second connotation only; that is, as a feature which varies from one kind of organism to another. Now, to use the above example, abdominal color is the character, which occurs in two "states" or alternatives, red and black.

For each character the states were coded: 1, 2, 3, etc. In the bee study the number of states per character ranged from two to eight. Much variation in the number of states is undesirable from the point of view of the methods discussed below. In the study we undertook most characters had either three or four states. However, when variation exceeds desirable bounds it might be preferable to divide the character state codes by a common denominator or to normalize them.

The kinds of characters used in the bee study and the manner in which they were coded are discussed at length by Michener and Sokal (1957). The possible effect of parallelism is also treated in the same article. For purposes of the present paper the available data might be summarized as follows: we have records of a given number (n) of species. For each species we have k records, k being the number of characters considered in the study. The coded values for any character may range from 1 to 9 depending on the number of states in which this character occurs in the group under consideration. As was mentioned previously it is desirable to have the number of states not differ too widely for the various characters. While it is not necessary to limit the number of possible character states to nine, our particular computational setup was greatly facilitated by the use of a single digit code.

PROCEDURES

Character correlations and species correlations

Two obvious ways suggested themselves to the authors regarding a procedure for deducing relationships from the character states of a group of species. We could either correlate characters with each other or species with each other. Since both of these methods would lead to interpretable, although differing, results a brief discussion of the implications of the two approaches follows.

Sturtevant (1942) undertook a study of the genus *Drosophila* with objectives and procedures somewhat similar to ours. He recorded 33 morphological, cytological and life history characters for each of 56 species of *Drosophila* and two species of the genus *Scaptomyza*. In his aim to develop a classification "as free from personal bias as I could make it," Sturtevant set up two tables. The first was a table of the total number of differences with respect to the 33 chosen characters between any two of the 58 species. These give the degree of difference between the species concerned and are

analogous to the complementary values of the "matching coefficient" discussed in the section on Choice of a Correlation Coefficient below.

A second table showed correlations between characters, expressed as two-way frequency distributions. By examining the three highest character correlations Sturtevant found that six species consistently fell into the exceptional classes of the two-way frequency distributions. They were the two *Scaptomyza* species and four species of *Drosophila* which he thereupon placed in separate subgenera. On the basis of the number of character differences between and within subgenera Sturtevant was able to confirm this classification and arrive at some ideas on the relationships and origins of the various groups. He also performed a similar analysis on 29 characters of 40 genera of flies (*Scatophaga*, *Conops* and 38 assorted Acalypterae) to establish the relations of the family Drosophilidae. Unfortunately the paper cited lists only summaries of the above tables and it is therefore difficult to compare Sturtevant's findings with ours.

Correlation between characters (R-technique in the idiom of the factor analysts) is the customary technique in biological and psychological studies involving correlational analysis. In character correlation matrices involving studies within one species each correlation represents the sum total of the common forces acting on any pair of characters. When analyzed by some method of factor analysis, the matrix customarily yields a so-called general size factor, a series of group factors affecting various groups of characters, and residual specific factors affecting single characters only. The foregoing is an example of a factor constellation involving morphological characters and is not necessarily the only possible constellation. As a matter of fact much psychometric work and the biometric papers by Howells (1951) and Stroud (1953) use the method of "simple structure" which *a priori* rejects solutions involving general factors.

Regardless of the constellation preferred, the factors common to two characters and causing them to be correlated could be visualized as developmental forces, genetic or environmental in the final analysis. The range of these genetic or environmental forces is dependent on the causes of variation within the sample of individuals studied. Thus a sample of individuals from an inbred, isogenic, line of animals would yield character correlations reflecting common nongenetic, physiological (*i. e.*, caused by microecological dif-

ferences) factors only. Another sample comprising individuals from various races or subspecies would provide correlations based on common factors representing (1) genetic differences between individuals; (2) genetic differences between races; (3) nongenetic physiological differences between individuals and (4) nongenetic ecological differences between races. One of the authors (R. R. S.) has been able to accumulate a series of character correlation matrices from various organisms representing these levels of variation. Matrices on correlation of aphid characters within galls (clones) and between galls have been published (Sokal, 1952) while similar matrices on aphid correlations between localities and morphological correlations within and between strains of houseflies and *Drosophila* await suitable analysis and publication.

When the sample transcends the bounds of the species the factors behind a character correlation matrix take on new meaning: They now represent genetic divergence or the results of evolutionary processes. In the one case they were ontogenetic forces, in the other they are phylogenetic forces. This type of analysis was pioneered by Stroud (1953) who analyzed correlations of 14 characters for soldiers of 48 species and imagines of 43 species of the termite genus *Kaloterms*. He was able to interpret some factors extracted from his correlation matrices as recognizable evolutionary trends.

Another method of correlational analysis is called the transposed matrix method or the Q-technique (as compared with the R-technique of character correlations, discussed above).³ It consists of correlations between individuals based on measurements of characters which they have in common. In psychology this involves correlations between persons based on scores for common tests which these persons have taken. In the Q-technique we are in effect dealing with the same kind of raw data as in the R-technique, but we compute the correlation coefficients by summing squares and products at right angles to the direction previously taken (or we transpose the matrix before computation which amounts to the same thing).

A Q-technique correlation coefficient in a study correlating individuals of one species represents common forces or factors acting on the two individuals concerned. In this case we cannot speak of the "sum total of common forces" as we could in the case of the

3. In a recent paper Cattell (1954) has suggested restricting the Q and R symbolism to studies involving factor analysis and proposed Q' and R' for studies, such as the present one, employing more superficial methods.

R-technique. Insofar as the characters used are indicative of the entire spectrum of potential variation of the individuals we can say that the resulting correlation coefficient is representative of the real affinity between two individuals. When scanned for clusters of high correlation coefficients the Q-type matrix reveals types of individuals which are similar. It is thus especially suited to classificatory problems. When subjected to factor analysis the resulting factors are now of a different nature. The general size factor has been lost and in its place we find a general taxonomic group factor which accounts for the overall correlations of all the individuals in the study.

When, as in the present study, the correlation is between species of a taxonomic unit the general factor is a general systematic factor denoting overall relationship within the systematic group. The species having the highest factor loading would be most representative of the group. Other factors would describe subgroups within the systematic unit and describe the relationships of these subgroups with each other and of the species to the subgroups. It should be clear from the above that for purposes of biological classification the relationships represented by a Q-technique matrix are more meaningful by far than are those of a R-technique matrix. Except for the above-mentioned work of Sturtevant (1942) which involved not correlations but character differences, the only Q-type study in systematics of which the authors are aware is in a publication by one of them (Sokal, 1958) containing factor analyses of selected portions of the present data. A number of the phytosociological coefficients of association and similarity can be considered as of the Q-type.

Psychologists have used Q-technique repeatedly (*e. g.*, Burt 1937, Stephenson 1936), although R-technique is still preferred in most studies. Cattell (1952) has listed 5 points of criticism of the Q-technique. It is appropriate that we discuss briefly their relation to the problems under study here. The first objection is that Q-technique loses the general size factor, yielding in its place a common species factor. This latter is claimed to be trivial by Cattell, and correctly so, for psychological work. However, in a matrix of correlations between species such a general systematic factor delineates the relation of individual species to the taxonomic group and indicates the proportion of the variance of each species explained by the general systematic factor.

Cattell's second objection to Q-technique is that it is unreasonable to assume simple structure in the factorization of a Q-matrix. The

authors agree with this argument, but for the purposes of the present paper it is not important since they are not here undertaking a factor analysis. Furthermore, they feel that simple structure (*i. e.*, each factor having essentially zero effects on certain species) is not necessarily a very suitable constellation for many biological factorizations.

The third objection refers to a customary shortcoming of Q-matrices. They are based on few individuals and generalizations about the entire population are drawn from them. In this study, the matrix is of course of more than adequate size. Furthermore our conclusions are not intended to extend to species not included in our study.

It is true that the species recorded are an eclectic sample from those extant in the world today. On the other hand we are of course dealing with a sample obtained by natural selection from the multitude of species or specieslike entities that have existed since the origin of the four genera of this study. Hypotheses regarding these extinct species will be valid only insofar as recent species reflect the course of evolutionary history.

Another point in connection with the third objection is the number of characters employed. True relationships will become apparent only insofar as the characters adequately represent the sources of variation within the species.

A fourth objection relates to the lack of equivalence in recording and interpreting the factors from the Q- and R-matrices. It compares the relative permanence of psychological tests with the relative impermanence of persons. In this study we are confronted with characters and species varying in their relative permanence, but both equally permanent when based on the time scale of the scientist investigating them.

The fifth criticism, labelling the Q-technique as descriptive rather than predictive, again is invalid when applied to the present data. Since the purpose of the study is historically descriptive and one of our aims is to divide the population of species into categories, the technique's fault for psychological research becomes a virtue in our field of investigation.

There are two evolutionary situations under which it is important to examine the two types of matrices. The first might be referred to as breakage of correlation. It occurs when in a certain evolutionary line two characters that were correlated in ancestral lines and are still correlated in related lines become independent of each

other. Under such conditions the R-matrix is a poor representation of the true relation between the two characters. There is no good way of representing such a correlation, close in one line, absent in the other. On the other hand a Q-matrix is not affected by such data.

Convergence of species for a number of characters is a second disturbing phenomenon. Here the R-matrix is not affected while the Q-matrix is affected if the convergent characters outweigh the nonconvergent ones in numbers.

We do not believe this is likely if an adequate number of characters is studied. In case of a preponderance of convergent characters and in the absence of paleontological data it is doubtful whether the systematists would be able to distinguish convergence from relationship by descent.

From a consideration of the above arguments it follows that given the objectives and material of the present study the Q-technique is to be preferred to the R-technique and the objections made by Cattell to the former method do not apply to our case. However, besides the theoretical reason for adopting the Q-technique as reflecting relationships between species there were several practical reasons for so doing. The problem of finding a suitable type of correlation coefficient between characters would have been formidable in view of the coding system adopted. Since some of the characters were present in two states only while others were present in as many as eight states, there would probably not have been any one type of correlation coefficient for all possible character combinations. A matrix based on correlation coefficients of different types would be far from desirable. Furthermore, uniformity of computational procedure was essential to efficient handling of the data by International Business Machines (IBM) equipment.

Not to be underestimated is the saving in computation resulting from adoption of a 97 x 97 species correlation matrix vs. a 122 x 122 character correlation matrix. The former requires the computation of only 4656 correlation coefficients while the latter would necessitate 7381 such coefficients.

The choice of a correlation coefficient

As a next step a suitable correlation coefficient had to be chosen to represent the correlations between species. There were serious considerations against the use of the product-moment correlation coefficient since the variables (species) are anything but normally distributed. Table 1 presents frequency distributions of state codes

TABLE 1

Frequency distributions of state codes for the characters of species 19, 56, 83 and 84.

State code	Sp. 19 f	Sp. 56 f	Sp. 83 f	Sp. 84 f
1	54	56	48	46
2	31	40	42	41
3	31	14	23	26
4	3	11	7	6
5	2	1	2	2
6				1
7	1			
Σf	122	122	122	122

for four representative species. The distributions are highly asymmetrical. Those for species 19 and 56 approach Poisson distributions for their means when the class codes are reduced by one. Any interpretation of this agreement is dubious, however, in view of the variable number of states possible per character.

Other correlation coefficients were considered and rejected. The correlation ratio, η , is unsuitable since ${}_x\eta_y$ does not necessarily equal ${}_y\eta_x$. Tetrachoric r would have lost some of the information available because it would necessitate reducing all characters to two states. Furthermore the theoretical assumptions of underlying normality essential to correct application of the tetrachoric correlation coefficient cannot be defended for all characters.

Another method of demonstrating an association between species would be the very simple one of counting the numbers of matches in states for the 122 characters of any pair of species of bees and then dividing this number by 122, the highest possible number of such matches. The results for species 19, 56, 83, and 84 are shown on table 2 where these "matching coefficients" are compared with product-moment correlation coefficients. The "matching coefficients" are somewhat higher than the correlation coefficients but resemble them in relative magnitude. In spite of this fact, "match-

TABLE 2

"Matching coefficients" (below diagonal) and product-moment correlation coefficients (above diagonal) between species 19, 56, 83 and 84.

	19	56	83	84
19	X	.40	.37	.37
56	.52	X	.47	.38
83	.53	.61	X	.93
84	.50	.54	.87	X

ing coefficients" were not used since they have an unknown sampling distribution, they distort resemblances by counting a 3 to 4 mismatch the equal of a 1 to 7 mismatch, and finally they would have been harder to handle by the IBM equipment available to us.

Lacking a more suitable means of correlation we adopted the product-moment r , in spite of nonnormal distribution of variates and possible heteroscedasticity. Various ways of improving the distributions by means of transformations were tried. Table 3 shows the same correlation coefficients as the upper half of the matrix of table 2, but based on $\sqrt{X}$ and $\sqrt{X+.5}$ transformations. The slight differences obtained do not justify the extra computational labor involved.

We have already briefly touched on the desirability of coding the data in such a way as to put all character states on the same scale. In a character with two states the code 2 indicates a situation differing greatly from one given by code 2 in a character with 7 states. This problem is also encountered in Q-matrices in psychology where the scores for different tests are often not in comparable units. This situation is usually met by normalizing the rows (tests, or in our case characters) of the raw score matrix. The authors did not per-

TABLE 3

Product-moment correlation coefficients between species 19, 56, 83 and 84 based on variates coded as $\sqrt{X}$ (below diagonal) and as $\sqrt{X+.5}$ (above diagonal). Compare with uncoded product-moment correlation coefficients in table 2.

	19	56	83	84
19	X	.42	.36	.37
56	.42	X	.50	.41
83	.36	.51	X	.93
84	.37	.41	.93	X

form this transformation since (1) it would have removed the common systematic factor from the matrix of correlations and would thus have lowered the correlation coefficients considerably; (2) application of the character state codes does standardize the data to a certain extent because 76 percent of the characters have either three or four states and only 3 percent have six or more states; (3) although the additional labor of normalizing the variates would not have been excessive the amount of IBM work involved in computing correlation coefficients would have been prohibitive, since a one-digit code would not have sufficed for normalized data.

The authors are well aware that their methodology of coding and correlation could profit by refinement. It is, however, our point of

view that in a pilot study of this nature such refinements are premature. Should the general method prove of value, significant results will surely emerge in spite of minor imperfections in technique.

Computation

The computation of a large matrix of correlation coefficients such as the 97 x 97 bee matrix presents serious technical difficulties. Only high speed electronic computing machines are able to perform this operation with real dispatch. At the time our bee data were being processed we had only punched-card tabulating machines at our disposal. It might be noted here that a computational operation of this magnitude cannot reasonably be undertaken without some automatic computing facilities. The equipment used by the authors is that available in the University of Kansas IBM laboratory: a card punch (type 26), a verifier (type 56), an accounting machine (type 402) and a reproducing machine (type 514).

The computational problem was simplified somewhat by the fact that the variates consisted of single digits only. This increased the number of variables that the machine could process simultaneously. Each IBM card represented a character with the state code of each species for the particular character listed in separate columns. Since there are only 80 columns per card, it was impossible to record all species on any one card. A different approach was therefore adopted and the card divided as follows:

Column 1—Project code

Columns 2-4—Character code number

Column 5—Deck code (explained below)

Columns 6-8—Left blank for possible subsequent use

Columns 9-44—Multiplier columns for 36 species

Columns 45-80—Multiplicand columns for 36 species.

The 97 species were divided into group I for species 1-36, group II for species 37-72 and group III for species 73-97. Since group III used only 25 columns another 5 columns were taken up by a repetition of data on species 1 through 5, which we used as a check on computational procedure. Six decks of 122 cards each, one card per character, were then prepared. The decks were constituted as follows:

Deck	Multiplier	Multiplicand
1	Group I	Group I
2	Group II	Group II
3	Group III	Group III
4	Group I	Group II
5	Group II	Group III
6	Group I	Group III

Different card colors besides a punched code were used to distinguish the decks.

By running these decks in succession through the tabulator we were able to reduce rewiring of the board to one half of what it would have been with the minimum number of decks (3).

The method of arriving at the Σx^2 and Σxy was the customary one of progressive digitizing with interspersed "X-cards." Running time on the 402 tabulator was some 24 hours. Punching and verifying of the cards had taken a similar amount of time. Thus the preparation of the Σx^2 and Σxy for the entire matrix took about a week. These values were computed for a half-matrix only. However, a test deck and five test variables detected wiring errors and machine malfunction with a reasonable limit of safety.

The next step was the computation of the correlation coefficients. This was done by computers using desk calculators.⁴ The matrix of squares and products was subdivided into manageable sections, 30 variables (species) square. All computations were checked by a different computer and, where possible, by different steps. The computational procedure employed was the customary L method.⁵ It does not seem necessary to elaborate on the details of this method. Any good textbook of statistics will contain a section on the computation of a product-moment correlation coefficient. Furthermore, each computation center has its own setup for correlation coefficients depending on the capabilities of the machines and thus no general account need be presented here.

The correlation coefficients were calculated to four significant decimal places and entered on a matrix. Three decimal places would have been quite sufficient for this study; however four were computed in case later statistical work required greater refinement. Total computation time for this phase of the work was 160 man-hours. It should be emphasized that the time estimates given above refer to the relatively simple equipment available to us. Digital computers are now available which would handle the entire computation, from raw data to completed correlation matrix without human intervention in less than an hour. This would be only one-two hundredths of the time it took us to compute the same informa-

4. The writers at this point wish to express their appreciation to Misses Betty Becker, Marion Clyma, Jacqueline Johnson, Normandie Morrison, and Messrs. D. A. Crossley, Jr., Ralph Jones and Roger Price for their conscientious assistance with IBM work and desk computation.

5. $r_{xy} = L_{xy} / \sqrt{L_x} \sqrt{L_y}$, where $L_{xy} = N\Sigma XY - \Sigma X\Sigma Y$ and $L_x = N\Sigma X^2 - (\Sigma X)^2$, $L_y = N\Sigma Y^2 - (\Sigma Y)^2$.

tion! With every passing year electronic computers are becoming more efficient and more widely distributed. Thus the computational aspects of our method will become a progressively less important impediment.

Since the matrix of correlation coefficients was unwieldy (it also had to be subdivided into sections) and since further work with the correlation coefficients was contemplated, the latter were punched on 4656 IBM cards, one to a card. These cards were duplicated by means of the reproducing punch in order to obtain cards for a complete matrix of 9312 correlation coefficients. Information on these cards included matrix row and column numbers for the particular correlation, the coefficient with sign, and a class code for the coefficient. These class code numbers (1-22) represented 22 classes of a frequency distribution of the correlation coefficients arrayed in ascending order of magnitude with class intervals of .05. In addition, the cards contained codes for the relationship between the two species involved as evaluated by conventional systematic methods (by C. D. M.).

The correlation coefficients on punched cards have so far been put to the following uses: We have compiled a printed tape record of the full matrix, column by column, which has been very useful for reference and further computation. Another tape has been compiled giving a listing and frequency distribution of the correlation coefficients grouped in the 22 size classes. This tape has been of great value in various approaches to a classification of the relationships demonstrated by the matrix. A third tape lists the sums of the correlation coefficients, column by column. This has been necessary for the B-coefficient method briefly described below. A fourth tape presents a two-way frequency distribution showing the relation between correlation coefficients and the relationship code developed by conventional systematic methods. These tapes were prepared in a few hours running time from the correlation coefficient cards, which we still expect to use in a variety of ways.

The matrix of correlation coefficients

In the bee study the 4656 correlation coefficients computed in the above manner ranged in magnitude from $-.0626$ for the correlation between species 26 and 92, to $.9747$ for the correlation between species 43 and 44.⁶ As was mentioned previously, a fre-

6. For lack of space the matrix cannot be reproduced here. Microfilm or IBM-tape or card copies can be obtained through the Secretary, Department of Entomology, University of Kansas, Lawrence.

quency distribution of these coefficients, grouped into 22 classes with class intervals of .05 was set up. The modal class showed a class mark of .38; this represents the most frequent class of correlation coefficients found between species in this study. However, a second mode was located at .78. This bimodality would indicate that we are dealing with two populations of correlation coefficients: those indicating close, possibly intrageneric relations and others representing more distant relations. Codes representing Michener's previous views on the relationships among the species were correlated with the above coefficients. The single correlation coefficient between the correlation matrix and Michener's codes was .80. It was encouraging to find that magnitude of the correlation coefficients in our matrix was apparently an estimate of systematic relationship as indicated by the previous classification.

Another way of examining these correlation coefficients is to study frequency distributions of the coefficients for any single species against all other species. By this means we were able to distinguish members of closely related groups of species from isolated species within a genus and these in turn from very isolated species representing monotypic genera or subgenera. For a detailed discussion and illustrations of this procedure, the reader is referred to Michener and Sokal (1957).

The absence of significant negative correlations from our matrix requires some discussion. Q-technique matrices of correlations between people (based on psychological tests) are quite likely to yield such correlations. If there are distinct, antithetical types of persons represented in the matrix, such as extroverts and introverts, it is likely that a high score for one type will be a low score for the other and vice versa. In our case evolutionary progress may be represented by either an increase or a decrease in state codes. In the majority of characters the supposedly primitive situation is an intermediate state code with two diverging evolutionary trends represented by the lower and higher code numbers. Furthermore, characters representing correlated trends were not necessarily coded along the same scale or in the same direction. It is clear that under such circumstances distantly related forms are likely to be uncorrelated rather than negatively correlated.

The search for group structure

The matrix of correlation coefficients between species can be put to a variety of uses and the analysis reported below represents merely an initial effort at an exploitation of the data. The correla-

tion coefficients serve as an absolute measure of relationship between any two species in our study, limited only insofar as the characters chosen do not represent the total correlated variation of the two species.

The search for structure among the correlation coefficients of the matrix is of course no different in aim from the search by the systematist for a natural system in an array of species. Such a system consists of a hierarchy of groups. Various methods can be used for discovering a hierarchy in data such as ours. A customary, rather simple device of the psychometrician is so-called "cluster analysis," developed to a fine art by Tryon (1939).

A concise description of the procedure (the ramifying linkage method) is given in Cattell (1944) and Thomson (1951). Because of the simplicity of the procedure, cluster methods are used extensively, although Cattell (1944, 1952) and others have pointed out that cluster analysis cannot be considered a substitute for the more involved factor analytic methods. Attempts to employ cluster analysis for finding structure in our matrix were only partially successful, since the resulting clusters were partly overlapping, *i. e.*, a given species might be a simultaneous member of two clusters. This makes good sense for intermediate forms in an abstract scheme of relationships. In a systematic hierarchic classification, however, groups at the same level have to be mutually exclusive for practical as well as for theoretical reasons, except for low level groups exhibiting reticulate evolutionary pattern (rare above the species level in animals). A further reason for the unsuitability of cluster analysis is the complexity of the clusters as more species are added to them. Although clusters are therefore not convenient in an initial search for structure, the diagram of relationships established by methods to be described below could be easily recognized in the clusters outlined by cluster analysis. A method essentially similar to cluster analysis is the ρ -group and ρF -group method of Olson and Miller (1951) applied to three paleontological R-technique matrices. It suffers from the same drawbacks as cluster analysis.⁷

7. After the present research and manuscript had been completed one of us (R. R. S.) became acquainted with the psychometric work of Professor Louis L. McQuitty of the Michigan State University, who in recent years has developed a whole battery of refined cluster methods (McQuitty, 1955, and a series of papers in press in *The British Journal of Statistical Psychology*, *Educational and Psychological Measurement*, and *Psychological Monographs*). Several of these papers deal with psychological problems which are closely related to those of biological classification. One of the methods invented by McQuitty bears a close resemblance to our variable group method developed below. It is interesting (as well as reassuring to us) that workers in different fields had unknown to each other developed some of the same formulations. We hope to try some of McQuitty's other methods on our material. They have the advantage of simplicity and can be programmed for electronic computation without much difficulty. Indeed the time may not be far off when computation for a study such as our bee work will be a minor matter routinely handled by a computing center in a very few hours and the remaining problem will be the collection of data for the machine and the interpretation of the voluminous answers that are produced.

As a technique for grouping the species we experimented extensively with the coefficient of belonging (B-coefficient) of Holzinger and Harman (1941). It is the sum of the correlations among the members of a group divided by the sum of the correlations of these group members with the other variables (species) of the study.

Results of our B-coefficient analyses for the bees were reasonably good, as judged by the previous classification and by our subsequent investigations. There was one main drawback, however. Large species groups showed a lack of structure and relatively low B-coefficients which would make the species in these groups appear a good deal less related to one another than members of groups of two or three species. The cause of this phenomenon is not hard to find. In large species groups the denominator of the B-coefficient would include high correlations due to correlations of group members with numerous other prospective members not yet included in the group. This would tend to depress the B-coefficient values. By the time all such members have been admitted to the group, it has become so large that even the admission of a relatively unrelated variable will effect the B-coefficient only slightly.

In view of the disadvantages of the B-coefficient we developed our procedure which is presented below in a general manner together with some of the reasons for its adoption. This presentation is followed by a detailed step-by-step account of the computational procedure for readers who wish to become more familiar with it.

A nucleus of a group was established, using the two species having the highest coefficient of correlation. Then species would be added to this nucleus, one at a time, always adding first the species having the highest average correlation with members of the group. The limit of the groups could be found by decreases ($\bar{L}_{n+1} - \bar{L}_n$) in the level of the average correlation $\bar{L}_n$, where the subscript refers to the number of members in the group. As in the B-coefficient a significant drop is empirically determined since sampling distributions of average correlations, such as $\bar{L}_n$, are unknown. By developing first lower groups (species groups), then by the same method grouping these into larger groups (sometimes subgenera), and these into still larger or higher groups, etc., it has been possible to develop a hierarchy of groups for which the diagram of relationships (figure 1) can serve as a representative. Each number in this figure represents a different species; for a list of the species concerned see Michener and Sokal (1957).

Since $\bar{L}_n$ is not amenable to rigorous statistical treatment it was decided to recompute correlation coefficients (using Spearman's sum

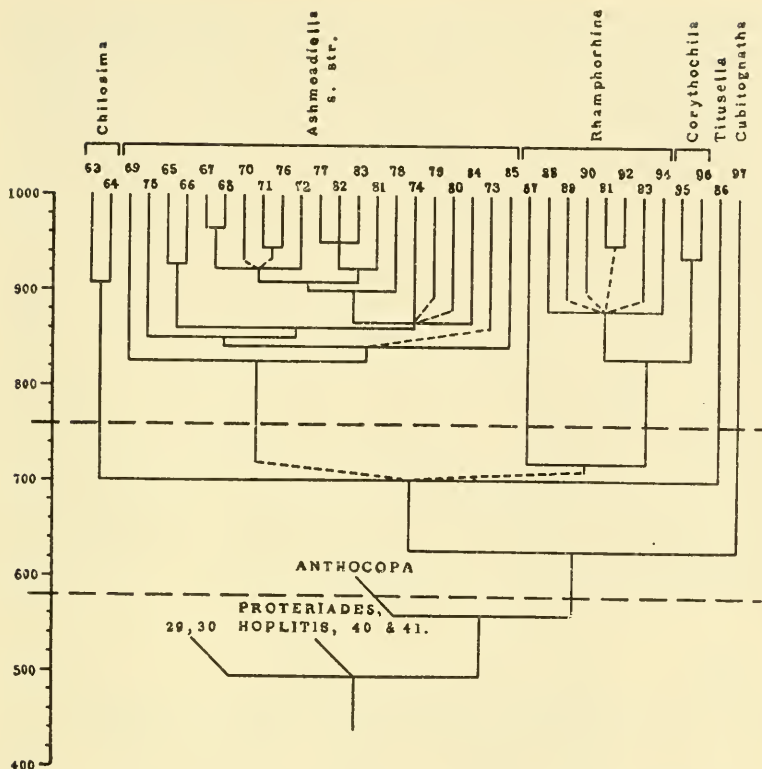


FIG. 1. Diagram of relationships for the genus *Ashmeadiella* obtained by the weighted variable group method. Ordinate: magnitude of correlation coefficient multiplied by 1000. Exact correlations between any two joining stems can be found by reading the value on the ordinate corresponding to the horizontal line connecting the stems. This value becomes approximate and maximal in cases of multifid furcations. Broken lines used where more than three stems join are for convenience only; the horizontal connecting line has the same significance as elsewhere. "Roofs" over species numbers at the summits of the lines delimit subgenera containing more than one species, as based on C. D. M.'s previous findings and not on this study. Generic names are in small capitals. The horizontal broken lines are not relevant to the present account; they are explained by Michener and Sokal (1957).

of variables method) after the group limits at each hierarchic level had been reached. Thus we returned at the end of each grouping procedure to a new matrix of correlation coefficients about which confidence statements might be made. Two further considerations in the final choice of a method for grouping remain to be mentioned:

We might have admitted only one new member for each group at a given hierarchic level, thus obtaining a diagram of relationships consisting of bifurcations only. We have called this method the

pair-group method as contrasted with the variable-group method, where any number of new members can be admitted to the group at any one hierarchic level, the limit of the group being determined by a significant drop in $\bar{L}_n$. The pair-group method has some theoretical justification in that much evolutionary ramification is believed based on speciation processes involving the splitting of one species into two. However, there must also occur some speciation as a result of the splitting of a species into more than two isolates and, on the assumption of equal evolutionary rates for these new lines, the pair-groups method would fail to represent the true situation. Moreover, many of the groups must be markedly different, not merely because of divergence, but because of extinctions of intermediates. A group might be broken into any number of different subgroups by different extinctions. Furthermore an empirical study of this method (see fig. 2 for an analysis of relationships in the subgenera *Chilosima* and *Ashmeadiella* by the pair-group method and compare with the left side of fig. 1 for the variable-group method) demonstrates that in spite of the pair-group device we are forced into multifurcations by drops in $\bar{L}_n$ too small to plot or by temporary

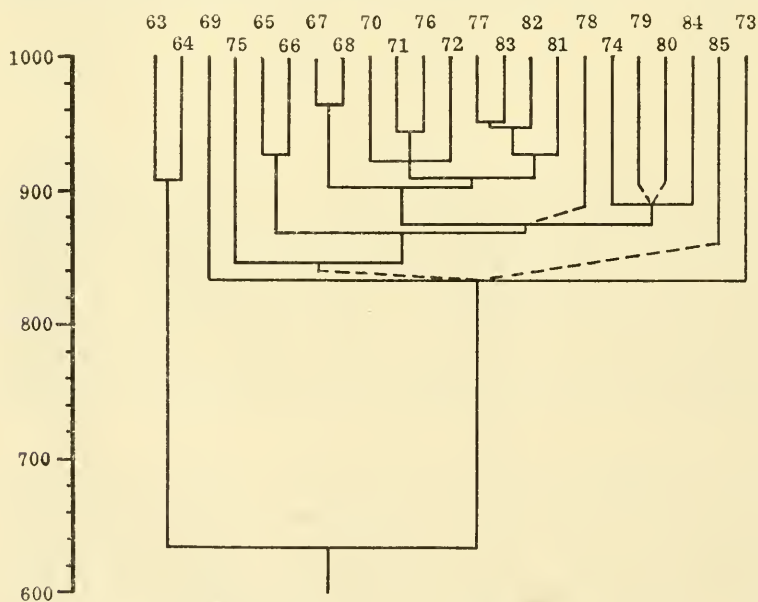


FIG. 2. Diagram of relationships for the subgenera *Chilosima* (63-64) and *Ashmeadiella* s. str. (65-85), obtained by the method of pair-groups, *i. e.* diagrams would ideally consist of bifurcations only. Stems have been weighted. Explanatory comments as for figure 1.

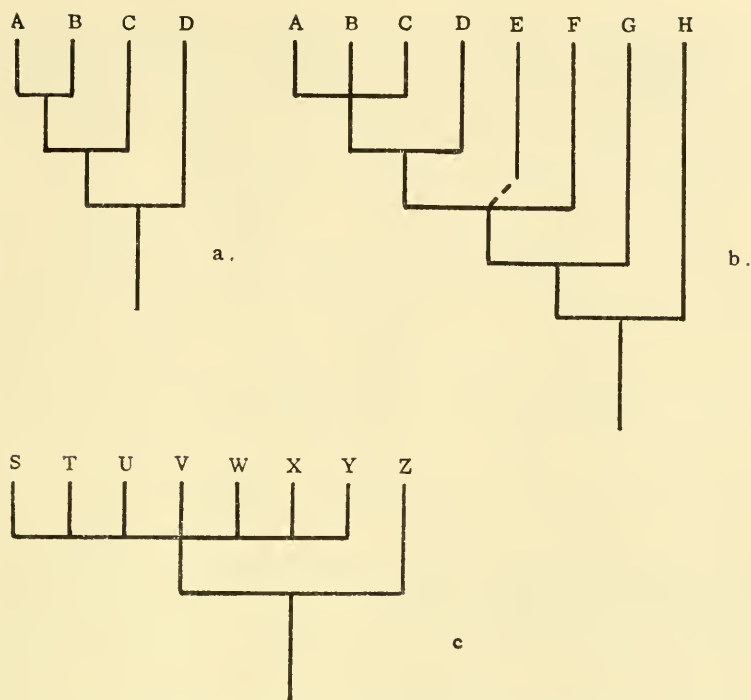


FIG. 3. Hypothetical diagrams of relationships to illustrate effects of different methods of weighting stems. For explanation see text.

reversals of $\bar{L}_n$ values, discussed below. Thus the variable-group method was adopted as the more reasonable and flexible of the two.

A second consideration is how to weight the variables during the recalculation of the correlation matrix after each grouping procedure. A simple diagram (fig. 3a) will make this issue clear. A and B represent the two species with the highest correlation coefficient. The $\bar{L}_n$ for C against A and B is significantly below r_{ab} , so that A and B are represented as being closer to each other than they are to C. When studying the relation of a fourth species D with group ABC we face the following problem: Should we calculate the correlation of ABC against D with A, B and C equally weighted or should we weight $A = B$ and $AB = C$? Rephrased biologically, the problem is whether to relate species D with the homogeneous group ABC, or with the stem AB-C, where C carries as much weight in determining the relation with D as do A and B together. Although in a simple case, such as the one described above the two alternatives may not produce very different results, in a situation such as de-

picted in fig. 3b species H might be weighted as $\frac{1}{3}$ of the group A-H, or $\frac{1}{2}$, depending on the system adopted. Similarly species B would be weighted $\frac{1}{3}$ in the former case but only $\frac{1}{2}$ in the latter case. When dealing with fairly large groups the second method would therefore reduce the weight of the early admitted members and increase the weight of those species admitted later.

The same problem is found in a situation such as shown in fig. 3c. By the first method species T is weighted $\frac{1}{3}$, by the second method it is weighted only $\frac{1}{4}$. Neither of the two methods is entirely satisfactory. By method one we are reducing the importance of species H and Z in representing groups A-H and S-Z respectively. If the relationship diagrams of figures 3b and 3c depict true phylogenetic relationships, then H and Z should represent half of their respective lines regardless of subsequent diversification in the other halves. On the other hand giving relatively greater weight to single late arrivals also gives heavier weight to specialized features of such species and thus would tend to distort the relational pattern, while specializations in the diversified branch of the stem tend to cancel each other, permitting a better average picture of the groups to emerge. The optimal system of weighting would be one between these two extremes, weighting each species according to its number of generalized and specialized features. This is clearly impossible without renewed introduction of a subjective element into our procedure. We therefore adopted the second method, *i. e.*, the weighting of new members as equal to the sum total of all old group members, thinking it to be the less objectionable of the two. We feel that this method will represent stems more correctly and that bias introduced by specializations of late joiners will be kept down by the large number of characters considered in our study.

We are reassured in our decision by the results of a comparative study on the subgenera *Chilosima* and *Ashmeadiella*. Figure 4 shows the results of a variable-group analysis of these subgenera by weighting method one, while results by method two can be seen in the left side of the diagram of fig. 1. General agreement as to relationships and level of furcations is very good. The main difference between the two diagrams is that in method one group 77-81⁸ first receives 79 before receiving group 67-72, 78 and 84, while in method two it first receives group 67-72, then 78 and then 79 among others.

8. In the interest of brevity groups will be identified by their leftmost (in the diagram) and rightmost members with a dash separating the two. Thus 77-81 means group 77, 82, 83, 81. It clearly does *not* include all species ranging in number from 77 through 81, and includes some beyond that numerical range.

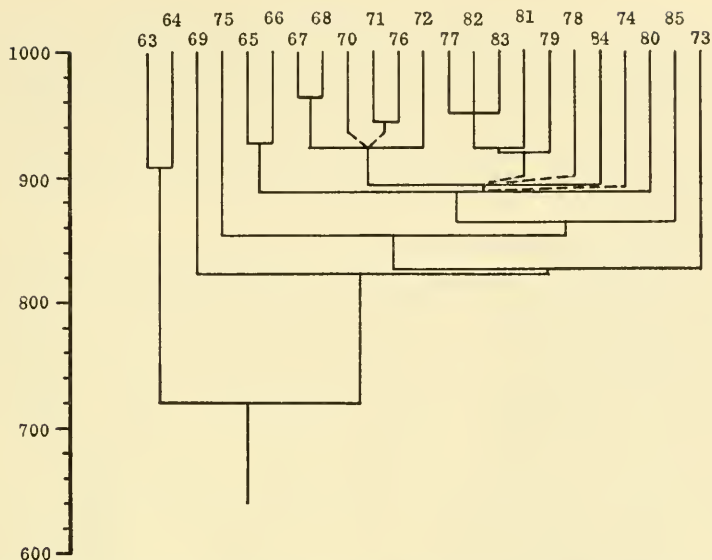


FIG. 4. Diagram of relationships for the subgenera *Chilosima* (63-64) and *Ashmeadiella s. str.* (65-85), obtained by the variable group procedure under weighting method one, *i. e.*, equal weights for all stems. Explanatory comments as for figure 1.

Careful examination of the original correlation coefficients makes the reasons for these differences clear. Group 77-81 is closer to 79 than to 78 except that 81 is closer to 78 than to 79. Also 81 is closer to 67-72 than are 77, 82, and 83. Therefore in method two, where 81 receives as much weight as 77, 82 and 83 together, 67-72 joins the nuclear group first. This is also partly due to the fact that unequal weighting of the species in the 67-72 group favors those close to the 77-81 group. Since 78 is closer to 67-72 than 79, the latter, while originally quite close to 77-81 is now temporarily delayed and 78 joins the combined group 67-81 before 79 does. These relations are at too low a phyletic level to be included in the original diagram of relationships drawn by C. D. M. who feels that there is little that can be obtained from classical systematic studies of these species to suggest whether method one or method two is preferable. In view of the small over-all differences between the two methods and especially in view of the fact that the lines concerned all join by either method with a difference in correlation coefficients of less than .06, it may well be that we have made too great an issue of the matter. In any case we feel confident that weighting method two will present us with a reasonably bias-free picture.

The Weighted Variable Group Method

It was thought advisable to give a detailed account of our method in order to enable readers to repeat the operations should they so desire. The subgenera *Chilosima* and *Ashmeadiella*, which have been used as a testing group before, will serve as an illustrative example. These subgenera include species 63 through 85 (see figure 1).

Correlation coefficients among these 23 species are shown in table 4. All values are significant with probability values of less than one percent. The highest correlation coefficient among these species is .965 for $\overline{67 \times 68}$.⁹ This is also the highest correlation involving either of these two species. The next to enter group 67-68 is species 70 which has the greatest average correlation ($\bar{L}_n = .892$) with 67 and 68 since $\overline{67 \times 70} = .896$ and $\overline{68 \times 70} = .889$. No other species in the study has as high an average correlation with 67-68, as can be learned from a few trials. We established empirically, as a result of numerous trials, that a drop in $\bar{L}_n$ of .030 gave a satisfactory limit for groups; therefore 70 is not to be admitted to group 67-68 at this particular time. Another high correlation involving species other than 67 and 68 is $\overline{77 \times 83} = .951$. This is also the highest correlation for the two species concerned. Next to join this nucleus is species 82 with an $\bar{L}_n$ value of .936. The drop is less than .030; therefore 82 is admitted. Next to join is species 79 with an $\bar{L}_n$ value against 77, 82 and 83 of .905. There is now a significant drop from the previous $\bar{L}_n$ value and 79 is excluded for the time being. Drops in $\bar{L}_n$ are always measured from the previous $\bar{L}_n$, not from the initial $\bar{L}_n$. Our second group is therefore 77-83. In a similar manner we established groups 63-64, 65-66 and 71-76, each consisting of only two species.

So far only 11 species out of the 23 of the study have been placed into groups. A systematic survey was then made of the remaining 12 species to see if any group had been missed. For example, examination of species 69 revealed that its highest correlation was with species 72 ($\overline{69 \times 72} = .820$). However, this latter value was not the highest correlation for 72, since $\overline{72 \times 76} = .904$. Thus 72 might eventually join the group containing 76 and 69 might join the group containing 72, both of which events came to pass at a later stage of the analysis. At the present time, however, species 69 and 72 are left unattached to any group. Similarly the remaining ten species in the study were shown not to belong to any nuclear group. To

9. We shall use this symbolism in place of the more formal $r_{67,68}$

TABLE 4.—Matrix of Correlation Coefficients Among Species 63 to 85
(Extracted from larger matrix of 97 species)

	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84																							
63.....	XXX																																												
64.....		.908	XXX																																										
65.....			.652	.653	XXX																																								
66.....				.624	.623	.927	XXX																																						
67.....					.692	.681	.806	.771	XXX																																				
68.....						.682	.672	.812	.767	.965	XXX																																		
69.....							.523	.511	.725	.676	.775	.817	XXX																																
70.....								.752	.718	.860	.832	.896	.889	.772	XXX																														
71.....									.685	.725	.831	.793	.804	.858	.728	.897	XXX																												
72.....										.669	.710	.839	.843	.849	.870	.820	.889	.902	XXX																										
73.....											.560	.611	.699	.620	.739	.719	.706	.727	.779	.789	XXX																								
74.....												.582	.637	.803	.731	.770	.758	.697	.748	.805	.779	.823	XXX																						
75.....													.569	.611	.786	.777	.737	.754	.771	.712	.771	.847	.683	.796	XXX																				
76.....														.697	.741	.837	.809	.883	.868	.734	.922	.945	.901	.751	.791	.752	XXX	XXX																	
77.....																.566	.608	.826	.784	.804	.833	.764	.780	.809	.861	.767	.862	.838	.798	XXX															
78.....																	.677	.719	.762	.718	.814	.792	.704	.848	.893	.811	.772	.762	.693	.895	.802	XXX													
79.....																		.567	.610	.830	.763	.748	.763	.768	.728	.764	.817	.772	.832	.826	.769	.926	.800	XXX											
80.....																			.643	.605	.822	.769	.787	.757	.716	.783	.828	.786	.789	.865	.802	.800	.863	.822	.852	XXX									
81.....																				.635	.679	.822	.788	.827	.847	.776	.842	.873	.866	.805	.834	.780	.872	.885	.883	.857	.816	XXX							
82.....																					.617	.661	.853	.783	.793	.816	.787	.821	.859	.888	.809	.857	.827	.850	.925	.844	.897	.855	.923	XXX					
83.....																						.589	.631	.866	.821	.815	.819	.738	.823	.861	.855	.762	.887	.821	.843	.951	.838	.891	.894	.907	.948	XXX			
84.....																							.542	.584	.794	.747	.725	.738	.659	.705	.740	.741	.667	.845	.766	.737	.886	.725	.852	.849	.788	.851	.926	XXX	
85.....																								.555	.605	.759	.695	.790	.819	.800	.774	.787	.854	.832	.843	.763	.784	.829	.723	.778	.762	.859	.849	.827	.744

set up one of the latter we required a correlation coefficient which was the highest one for both participating species (*i. e.*, the reciprocally highest correlation).

After the groups had been delimited a new correlation matrix was computed considering the newly formed groups as single variables, *i. e.*, the previous matrix of 23 variables (matrix 1) was reduced to one of 17 variables (matrix 2). It is self-evident that the only correlation coefficients in need of recomputation were those involving new groups. Correlations involving only species that had remained single were not altered in any way. As a matter of fact, a procedure was devised by means of which the correlations were not even recopied, but variables joined into groups were crossed out and the new group variables were entered along the margins of the old matrix. The actual computational procedure is quite simple and considerably less complicated than the computations for finding the original correlation coefficients. It is described in the paper by its originator (Spearman, 1913) and also by Holzinger and Harman (1941). Let us illustrate this method by computing the correlation between groups $(63)_1$ and $(67)_1$ ¹⁰. The general formula for this computation is

$$r_{q.Q} = \frac{\square qQ}{\sqrt{q + 2\Delta q} \sqrt{Q + 2\Delta Q}}$$

where $\square qQ$ is the sum of all correlations between members of one group with the other group, Δq is the sum of all correlations between members of the first group, ΔQ is a similar sum between members of the second group, q is the number of species in group one and Q the number of species in group 2. Thus in this particular case $\square qQ$ equals $(63 \times 67) + (63 \times 68) + (64 \times 67) + (64 \times 68) = .692 + .682 + .681 + .672 = 2.727$; Δq in this case equals only $(63 \times 64) = .908$ while ΔQ equals $67 \times 68 = .965$, since each of these groups consists of two species only. In cases where a group consists of 3 species, for example, the Δ term consists of the sum of $(1 \times 2) + (1 \times 3) + (2 \times 3)$. In the present case $q = Q = 2$ species. Substituting into the formula given above:

$$(63)_1 \times (67)_1 = \frac{2.727}{\sqrt{2 + 2(.908)} \sqrt{2 + 2(.965)}} = .704$$

10. The notation $(63)_1$, refers to the group of species formed in matrix 1, the lowest numbered member of which is species 63, *i. e.*, to group 63-64. Similarly $(67)_1$, refers to 67-68, and $(77)_1$, to 77-82-83.

These computations can be set up in a systematic manner and are then neither particularly complicated nor time consuming. In the special case where we wish to calculate the correlation coefficient between a single species (x) and a new group (q), the formula is amended as follows:

$$r_{x,q} = \frac{\Sigma r_{x,q}}{\sqrt{q + 2\Delta q}}$$

An illustration is the correlation of species 69 with group $(77)_1$. $\Sigma r_{x,q}$ equals $(69 \times 77) + (69 \times 82) + (69 \times 83) = .764 + .788 + .738 = 2.290$, while $\Delta q = \frac{(77 \times 82)}{2} + \frac{(77 \times 83)}{2} + \frac{(82 \times 83)}{2} = .925 + .951 + .948 = 2.824$.

$$\text{Then } \frac{69 \times (77)_1}{\sqrt{3 + 2(2.824)}} = .779$$

In such a manner a new 17 x 17 correlation matrix (matrix 2) was constituted. From this point on the species groups $[(63)_1, (65)_1, (67)_1, (71)_1, \text{ and } (77)_1]$ were tested as though they were single species.

Once matrix 2 had been computed the identical grouping procedure was followed. Group $(71)_1$ had a mutually highest correlation with species 70 at .923. They were then joined by 72 and group $(67)_1$ at $\bar{L}_n$ levels of .903 and .885 respectively. These affiliations of 72 and $(67)_1$ were also their highest correlations. The next prospective joiner was species 81 at $\bar{L}_n = .859$, *i. e.* not quite the established drop of .030. However species 81 had highest relations not with the previous species but with group $(77)_1$ with a correlation of .923. Therefore it was excluded from consideration as a candidate for the earlier group and the runner up, species 78, used instead. The latter gave an $\bar{L}_n$ value of .844, clearly a significant drop from .885. Species 81 meanwhile was used in a nucleus of a new group $77-81[(77)_2]$. Situations such as the above were the exception. In general the relations and choices were entirely straightforward and could be left to the discretion of the computing assistants.

At the end of each grouping procedure the remaining single variables were checked to avoid missing groups with low correlations between members. With each grouping procedure the matrix of correlation coefficients became smaller and the job of recomputation less. The weighting procedure adopted by us was automatic in that all correlation coefficients used were from the previous matrix and not the initial one. It took eleven matrices to obtain a single

group out of the 23 species of the two subgenera. This amount of work could have been reduced by raising the minimum recognized difference in $\bar{L}_n$ level above .030 but there would have been a resulting loss of detail in the diagram of relationships. Conversely, however, reducing the recognized difference below .030 would not have increased the meaningful detail, since even .030 was too small to prevent the occasional reversal of r values discussed below.

Once computed, the relations were represented as diagrams of relationships as in figure 1. The ordinate at the left of each diagram is graduated in units of $1000 \times r$. The correlations between any joining stems in the diagram can be read by measuring the level along the ordinate of the horizontal line connecting the stems. Thus species 63 and 64 are correlated at a level of .908, while group 63-64 is related to group 67-72 at .702. Furcations involving more than three lines are shown by broken lines converging on the midpoint of the horizontal line as in group 88-96 of the above figure. The tops of the figures are at a level of 1000 (correlation of 1) since obviously each species is perfectly correlated with itself.

In cases of groups of only two stems the $\bar{L}_n$ level corresponds to the correlation coefficient of the two stems. When more than two stems join to form a group the highest $\bar{L}_n$ level was graphed for all group members. Thus while 77×83 equals .951, $\bar{L}_n$ for 82 against 77 and 83 equals .936. The group of these three species (77-83) is shown related at levels .951. Occasionally the correlation coefficients for the same group in successive matrices will rise a little. Thus in this same figure groups 63-64, 69-85, 87-96, and species 86 are shown joining at .702. The first three groups actually joined at .671, but species 86 which joined their group at the next matrix did so at level .702. This type of situation, which occurred infrequently, might lead one to express concern about the validity of the method, since regular decreases in levels of correlation coefficients and $\bar{L}_n$ values are expected. However, it can be shown from Spearman's formula for the correlation of sums of variables that slight increases in the levels of correlation coefficients of the sums of variables above the correlations of their component variables are possible. For example, if A and B have formed the nucleus of a group at $r_{a \cdot b} = .9$ and C is about to join them, then by the rules of the variable group method both $r_{a \cdot c}$ and $r_{b \cdot c}$ must $< r_{a \cdot b} = .9$. It can then be shown that $r_{(ab) \cdot c}$ must be $< .925$. Thus $r_{ab \cdot c}$, while it will usually be $< r_{a \cdot b}$, could be slightly more than .9. Similar situations can be shown to exist with larger-sized groups. The increases found by us were well

below the mathematically possible limits. In all such cases the relations were represented as multifid furcations of all the stems involved in the reversal and at the highest of the several $\bar{L}_n$ levels considered.

In a successful method of studying relationships, the results of the analysis should be relatively independent of the number of species in the correlation matrix. If at least one species per species-group is included in a matrix, the ideal method of analysis should reproduce the diagram of relationships based on an earlier study of a larger matrix. If the method can be shown to produce similar results, the fact that our matrix contains only a sample from the population of species can be ignored with greater assurance.

We tested this question by subjecting the odd-numbered species in the entire genus *Ashmeadiella* to a weighted variable group analysis. This should give an adequate cross-section of relationships in that genus. Since some trends might be lost by exclusion of the

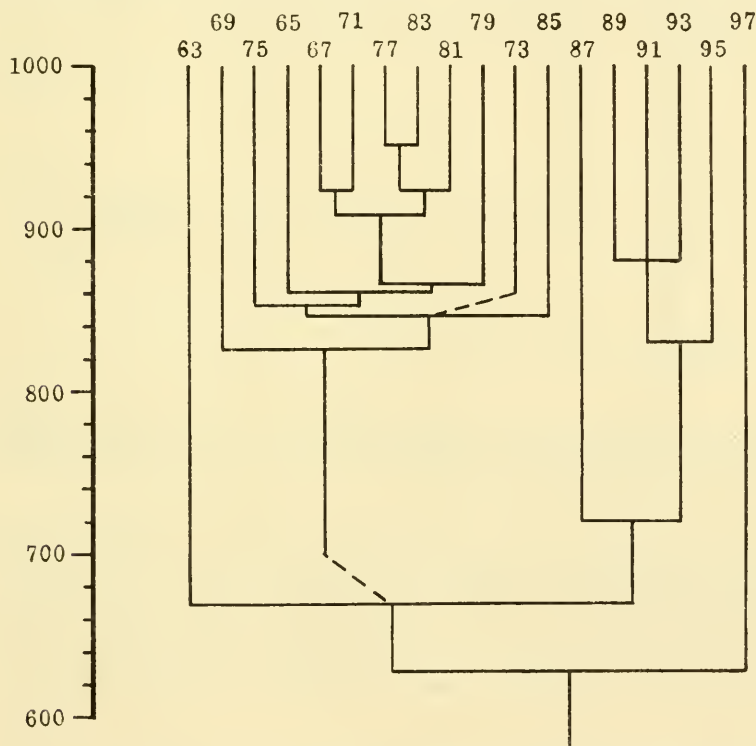


FIG. 5. Diagram of relationships predicted for odd numbered species of the genus *Ashmeadiella* on the basis of the relationship diagram of figure 1. Explanatory comments as for figure 1.

even-numbered species a special diagram of relationships was prepared from figure 1 by using only odd-numbered species. Figure 5 shows this predicted diagram of relationships.

Figure 6 shows the results of the weighted variable group analysis on the odd-numbered species. There is less structure in this dia-

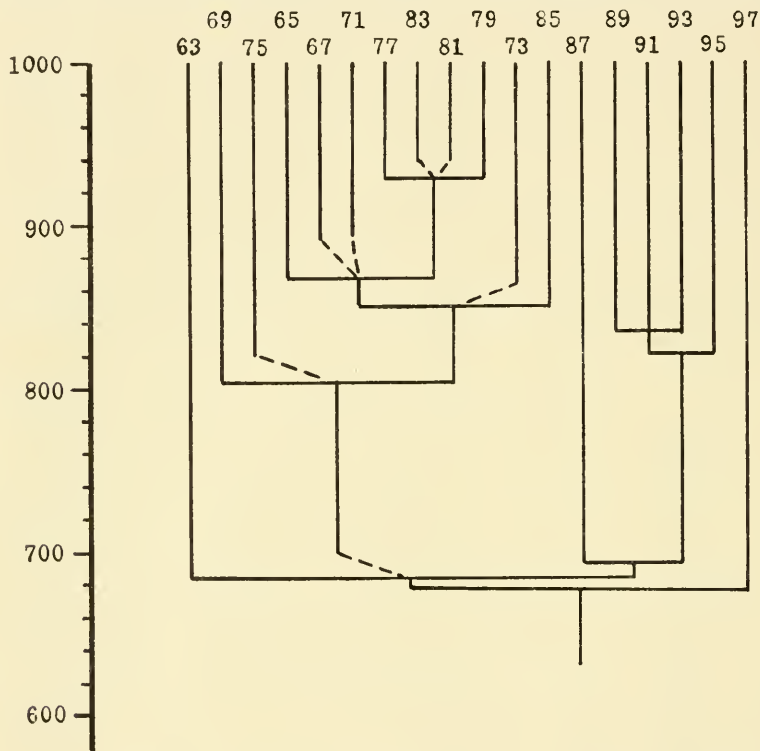


FIG. 6. Diagram of relationships obtained by an independent weighted variable group analysis of the odd-numbered species of the genus *Ashmeadiella*. Explanatory comments as for figure 1.

gram as compared with the predicted diagram of Figure 5. This was to be expected since some of the structure was based on relations involving the missing even-numbered species. In general, agreement between the two diagrams is very good, however, and we therefore feel reassured that the species left out in our study would not have changed greatly our diagrams of relationships.

CONCLUDING COMMENTS

A detailed discussion of the comparisons of our findings with the previous classifications of the four genera of bees is given by Michener and Sokal (1957). It will suffice here to state that general agreement was good but that a number of taxonomic re-evaluations seemed necessary as an outcome of these analyses. It should be remembered that while diagrams such as figure 1 may suggest phylogenies, in reality they only indicate static relationships. As indicated in the paper referred to, additional refinements were devised to give diagrams of relationships which we believe more nearly approach phylogenetic trees.

In view of these results we are encouraged to believe that, since the methods we have described are increasingly practical with the growing availability of high speed computers, this or similar schemes will be more widely utilized with different groups of organisms. Although the method we have described is a first attempt and would profit by either simplification or refinement, we believe it is a step toward reducing the subjectivity of systematic work, and therefore a step in the right direction.

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The Role of Tissue Spaces and Nerve Fibers in the Spread of Tetanus Toxin in the Rat

BY

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ABSTRACT. The extensive review of the literature on all phases of the tetanus problem reveals there is general agreement as to the etiology, pathogenicity, immunology and treatment of the disease. However, the mode of transport of the toxin in the body and its site of action are not fully understood. The following four pathways have been suggested by various workers: vascular stream, axons, lymphatics of peripheral nerves and tissue spaces of peripheral nerves.

Intraneural or intramuscular injection of toxin results in local tetanus. This is characterized by a segmental progressive involvement of musculature beginning with muscle groups in the injected extremity. Blood-borne tetanus follows intravascular inoculation and always results in involvement of the facial and masticatory muscles first despite the site of injection. Blood-borne tetanus appears following intramuscular injection if the epineurium is removed and the perineurium teased open in the nerves to those muscles. However, if antitoxin is also administered intravenously no symptoms of tetanus develop. Intravascular antitoxin does not prevent the onset of local tetanus if the nerve sheaths are intact. Local tetanus results from injection of toxin intramuscularly in the absence of nerve fibers to those muscles. However, the epineural sheath must be intact. The results of these experiments suggest that the primary path to the central nervous system for tetanus toxin is by way of the tissue spaces of peripheral nerves.

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INTRODUCTION

The current literature reveals that considerable clinical and experimental work is still being carried out on tetanus, however, the knowledge of its etiology has changed little since the time of Hippocrates (Singer, '28; Chadwich, '50). It is probable that its characteristic symptoms were known even prior to that time. The treatment of tetanus in the early part of this century was empirical, and to a certain extent remains so today (Adams, 1856; Rose, 1897; Abel and Hampil, '35; Nielsen, '51; Melbourne Pediatric Society, '53; Chackleton, '54; Drew, '54; Bucco, '54; Hampton, '54). No agreement has ever been reached on all aspects of the etiology of tetanus (Brunner, 1894; Rose, 1897; Meyer and Ransom, '03; Abel and Hampil, '35; Doerr et al '35a, b; Penitshka, '53; Drew, '54; Wright, G. P. '54).

The extensive literature prior to the discovery of *Clostridium tetani* by Nicolaier in 1884 was partly summarized by Hutchinson and Jackson (1861), Brunner (1894), Rose (1897) and von Behring ('04). Curling's attitude is representative of that era. He stated that tetanus is a disease of the nervous system (Curling, 1836). Objections were raised against this theory (Heiberg, 1861). (For further discussion see review article of Abel and Hampil, '35.) Simpson recognized that the poison is produced at the site of the wound (Humphreys, '35). Carle and Rattone in 1884 successfully transferred the infectious agent, and the same year Nicolaier identified the bacillus in mixed cultures. Pure cultures were obtained by Kitasato (a and b) in 1889 whereas Faber in 1890 induced tetanus with germ-free filtrates and immunity was demonstrated by von Behring and Kitasato in 1890. They also discovered the antitoxin (Kitasato, 1891; Kitasato, 1892; von Behring, 1892), and thus closed the period (1884-1891) in which most of the bacteriological and immunological factors were ascertained.

The new century began in which success in prophylaxis (Abel and Hampil, '35; Boyd, '46; Long and Sartwell, '47; Vit. Stat. of the U. S., '50; D'Antona, '52; Melbourne Pediatrics Society, '53; Ramon, '53; Lancaster, '53; Slome, '54 and Major, '54), and improvement in management of the disease (Lanfranchi, 1295; Humphrey, 1856; Meltzer and Aver, '05-'06; Buxton and Kurman, '45; Torrens, Edwards and Wood, '48; McDonald, '49; McIntyre, '49; Nielsen, '51; Raynaud and Wright, '53; Melbourne Pediatrics Society, '53; Chesni, '53; Benbanaste, '54; Chackleton, '54; Bucco, '54; Schubert, '54; Drew, '54) was achieved, however, the manner of distribution of

the toxin in the infected organism, its mode of action and the cause of localized and generalized symptoms in tetanus are still not fully understood.

A. Bacteriology, Immunology and Toxicity

Clostridium tetani is described as slightly motile in vegetative forms, gram positive, anaerobic and a slender bacillus which produces highly resistant spores. The dimensions are 0.3 to 0.5 μ in width and 2 to 5 μ in length, but vegetative filaments of much greater length occur. The spores are spherical, terminal, and wider than the bacillus, which has a characteristic drumstick shape. The bacilli are arranged singly or occasionally in chains. Isolated colonies in deep dextrose agar have a wooly appearance and may either be flocculent or with an opaque center. Surface colonies are flat, rhizoid, or even feathery, and frequently colonies on blood agar exhibit hemolysis (Burrows, '50). The growth requirements of *Clostridium tetani* and factors in toxin formation were recently extensively studied by Fildes ('25-'29) and Mueller and his co-workers (Fisek, Feeney, Miller, '42-'54; Ehrismann, '37 and others). MacLennan ('39) on the basis of specific flagellar antigens differentiated by agglutination ten types of *Clostridium tetani*. Toxin produced by all forms of *Clostridium tetani* is identical and is neutralized by one antitoxin. Antibacterial sera contain agglutinins and opsonins specific to each type.

Von Behring and Kitasato (1890) demonstrated that filtrates of the cultures contained toxin, which may be separated from the bacteria by filtering through Berkefeld and Chamberland filters. The toxin diffuses from within the cell in the surrounding medium (Stone, '54) and is probably protein in nature (Eaton, '36). In purified form the protein minimum molecular weight is about 67,000 (Pillemer, Wittler, Burrell and Grossberg, '48); however, component structure and qualitative differences were postulated (Friedemann and Hollander, '43a; Haku, '39; Aristovsky et al '38 and others). Imbriano ('50a) describes the tetanus toxin as a protein with neutral reaction. It is composed of simple alpha amino acids such as dicarboxylic amino acids (glutamic and aspartic) and basic amino acids such as hystidine. It probably contains another amino acid such as serin or threonine. Tetanus toxin does not have in its structure homocyclic amino acids such as phenylalanine and tyrosine or heterocyclic amino acids such as tryptophane. Ehrlich in 1898 separated the tetanus endotoxin into two compounds, the tetanolysin and tetanospasmin.

No specific characteristic action of the endotoxin is known, however, lethal doses produce the usual symptoms of endotoxin intoxication (Burrows, '50). Concentrated solutions of toxin show hemolytic activity which is due either to enzymatic action on plasma lecithin, producing lysolecithins in the first stage, or to esterase and protease action on the lipoprotein membrane of the erythrocytes. Tetanus toxin loses its hemolytic activity *in vitro* and its antihemolytic activity *in vivo* when it is transformed into toxoid. Antisera, penicillin G, antilipases (quinine salts) and antioxidants (nordihydroquaiaretic acid) inhibits or retards hemolysis (Imbriano, '50b). The tetanolysin causes hemolysis of red blood corpuscles. It induces antihemolysin production and seems more thermolabile than tetanospasmin (Zinsser and Bayne-Jones, '39). The diffusion constant of tetanolysin is 0.037 (Porter, '47). Some nonpathogenic strains produce tetanolysin (Kerrin, '30; Hall, '30). Roux and Borrel (1898) demonstrated that tetanospasmin has a strong affinity for nervous tissue. Meyer and Ransom ('03) showed that the toxin once fixed by the nervous tissue cannot be neutralized. Abel, Hampil, Jonas, and Chalian ('38) found that when three lethal doses of the toxin were injected intravenously, the irreversible fixation of one lethal dose was completed in the relatively short time of 5 to 7 hours. Recently Wright, E. A. ('54) demonstrated the rapidity of fixation of the toxin in the guinea pig's medulla oblongata. He states that at least one fatal dose becomes fixed in less than 30 minutes following injection of 100 lethal doses. The high toxicity is apparent from the fact that as little as 0.000013 gamma of the crystalline toxin prepared by Pillemer, Wittler and Grossberg in 1946 was able to produce tetanus in mice after intramuscular injection. The purified toxin contains about 6,400,000 lethal mouse doses per milligram. Using cold methanol Pillemer, Wittler, Burrell and Grossberg ('48) prepared a toxin that is lethal to mice in doses of 0.09×10^{-3} μ g.

The toxin is destroyed by proteolytic enzymes, and an aqueous solution of tetanus is highly unstable to heat and light (Dubos, '52). It is inactivated by ultraviolet light (Courmont and Nogier, '09a, b), exposure to Beta-rays (Baker, '35), hydrostatic pressure (Basset, Machebouef and Wollman, '37) and *in vitro* by vitamin C (Jungeblut, '37). (For further references concerning the stability of the toxin see Porter, '47, or original papers.) Imbriano ('50c), studying the enzymatic properties of tetanus toxin observed no carbohydrazic, phosphatasic, oxidasic and peroxidasic properties, how-

ever, he observed proteasic action on gelatine and an esterase, lipase and lecithinase activity. The toxin hydrolyzes the fatty acid fraction of lecithin but does not act on the glycerophosphoric part. The esterase activity is zero at 0°C. and increases progressively with an increase in temperature (up to 40°C.). The inoculation of an incubated lecithin-tetanus toxin mixture does not produce tetanus in rats. The lecithin is hydrolyzed by the tetanus toxin effectively destroying its toxicity.

Requirements for toxin production were described by Mueller and associates ('42-'54), Fildes ('25-'29), Knight and Fildes ('30) and Campbell and Fildes ('31). They pointed out the dependence of spore germination on the oxidation-reduction potential of the tissues. The genesis of tetanus in the body is broadly discussed by Topley and Wilson (Wilson and Miles, '46). They conclude that the presence of suitable accessory factors enable the spores to germinate and multiply in the tissues. It seems probable that this action is dependent on the formation of an area of necrosis in the tissue with sufficiently low oxidation-reduction potential to permit the spores to germinate. Pelloja and Tusini ('50) found that the course of experimental infection appeared to be aggravated by the presence of destructive lesions, especially of the muscles. Histamine has no influence on the progress of experimental tetanus, therefore, the symptoms of tetanus are not considered to be due to the liberation of histamine by the injured tissues.

Von Behring and Kitasato (1890) in a series of ingenious experiments demonstrated active immunity by injecting animals with modified toxin treated with a solution of iodine trichloride. Passive immunity was obtained by injecting sera of actively immunized animals (Kitasato, 1889 a, b; von Behring and Kitasato, 1890; Kitasato and Weyl, 1890; Kitasato, 1891; Kitasato, 1892; von Behring, 1892 and Kitasato, 1893). Topley and Wilson (Wilson and Miles, '46) described the antitoxin as being fairly stable in cold and in the absence of light. Exposure to sunlight or diffuse daylight gradually destroys it. It resists heat at 60°C. for half an hour but is partly destroyed at 65°C and completely at 68°C. (Tizzoni and Cattani, 1890). The antitoxin is nondialysable and is precipitated by ammonium sulphate. Hydrochloric and lactic acids and caustic potash destroy it. The antitoxin is standardized. The American unit of antitoxin is defined as 10 times the least amount of serum necessary to save the life of a 350 gram guinea pig for 96 hours against the standard test dose of toxin. The standard dose of toxin

is 100 MLD of a standard toxin preserved at the National Institute of Health, Washington. The permanent Committee on Standardization of the League of Nations (Prausnitz, '29) has suggested an International Standard Unit equivalent to one half an American unit and based on standard antitoxin kept at the Serum Institute in Copenhagen (Dubos, '52).

The therapeutic and immunological value of immune serum has been extensively studied. The immunity thus obtained is of short duration (McConkey and Homer, '17), and of doubtful therapeutic value (Korganova-Myuller, '40), however, good results have been reported following intrathecal administration in animals (Sherrington, '17) and man (Yodth, '32). Others pointed out the danger of intrathecal administration (Wainwright, '26; Spaeth, '41a, b and others). The intravenous route was preferred by other groups (Florey and Fildes, '27) especially after Abel's blood transport theory was introduced in 1934. Bruce ('20) points out the effectiveness of tetanus antitoxin therapy and prophylaxis during the years 1914-1918. The incidence in British war wounded in 1914-1918 was 1.17 per 1,000 while mortality in pre serum days was about 85%. According to Major ('54), the records in the Surgeon General's Office in Washington show only four deaths from tetanus from April 17, 1917 to December 31, 1919 in the American Army where prophylaxis was introduced. During the American Civil War, less than two in 100,000 developed the disease. Bruce ('20) found that the incubation period was prolonged and there were fewer fatalities among persons who received antitoxin prophylaxis treatment. Dosage requirements were higher and success depended on the time of administration. Abel and Chalian ('38) pointed out that neutralization is confined to the nonfixed but already absorbed toxin in the nervous tissue. Russe ('50) presents a survey of the records from 10,250 patients who had tetanus antitoxin for prophylactic purposes. The data showed that 3.9% of the cases had serum reactions. No fatalities resulted from these reactions. D'Antona and Valensin ('37) and many other investigators pointed out the greater value of active immunization over passive. Consequently, the value of antitoxin serum prophylaxis became the subject of a controversy. It was suggested it be used immediately with wound treatment (Milkó, '40) and in combination with tetanus toxoid (Firor, '39).

Pettavel ('40) reviews the history of active immunization since 1917 when Bazy inoculated soldiers with iodine treated tetanus

toxin. D'Antona ('52) reviewed the important literature on prophylaxis and immunity during the period 1923-1951. Since the formaldehyde treated toxoid was prepared by Descombey in 1924 and aluminium precipitated toxoid by Bergey (1934) and Jones and Moss (1936), active immunization found extensive use in prophylaxis (Ramon, '53). The use of toxoid in treatment was also studied (Raynaud and Wright, '53) and protection of short duration was found. The lethal effect of toxin can be prevented or delayed by large doses of tetanus toxoid alone given 1 or 2 days previous to the administration of the toxin. The explanation suggested is a blocking by the toxoid of a hypothetical substance in the C. N. S. which would otherwise react with the toxin and produce nerve cell damage. Another explanation is that there is a competitive inhibition of the action of the toxin. The British regulations for standardization require that more than 9 guinea pigs must be injected with five times the human dose, and that after 6 weeks at least two thirds of the guinea pigs must contain a minimum of 0.1 A. U. per ml. of blood serum (Topley and Wilson, see Wilson and Miles, '46). Since no international standard exists for tetanus toxoid, the United States Army specified that the toxin contain at least 10,000 guinea pig MLD's per ml. and be detoxified with 0.4 per cent formalin. The final preparation must be atoxic for guinea pigs in 5 ml. amounts, and guinea pigs receiving 1 ml. as an immunizing dose must be able to withstand 10 MLD of toxin six week later. (Long, '43, cited by Burrows, '50.) Surjan, Richter and Rethly ('54a, b) purified and concentrated tetanus toxoid with trichloroacetic acid and obtained toxoid which contained a grade of purity: 250-940 Lf/mg. N., and 200-900 Lf/mg. N. Delsal and Mir ('54) also obtained high concentration and purity by freezing at -15° C. The toxoid was precipitated with trichloroacetic acid at pH4. Ipsen ('54) concludes that no correlation exists between susceptibility to toxin and immunizability to toxoid. Multiple inoculations were recommended for high titer and long lasting antisera (Kestermann, Schleining and Voght, '39). Different methods were adopted in the British army (Boyd, '38; Boyd and MacLennan, '42). Wolters and Fiscoeder ('53) investigated the value of an aluminium-absorbed prophylactic and found that after two injections at 4-week intervals a basal immunity lasting at least 10 years was produced. A later inoculation of a booster dose resulted in the production of circulating antitoxins even within the shortest incubation period of tetanus. Similar conclusions were previously drawn by Bigler ('51) and others. Com-

bined inoculations of tetanus toxoid with pertussis and diphtheria prophylactic (Faerber, '53), or with typhoid-paratyphoid vaccine (Maclean and Holt, '40), are common. Inoculations at birth with diphtheria, pertussis and tetanus was described by Chamberlain and Bullock ('50). War records or reports from territories where active immunization is obligatory, reveal that by proper immunization tetanus can be completely prevented. For instance, among 16,000 wounded in the British Expeditionary Force in France no cases of tetanus occurred (Bensted, '40). Long and Sartwell ('47) state that in the period of 1942-45 only 12 cases of tetanus occurred in the United States Army of which 6 were nonimmunized persons. There were 4 cases in the United States Navy of which 3 were non-immunized persons. Similar excellent results were obtained in the civilian population where the inoculation with tetanus and diphtheria prophylactic were made compulsory, e. g. France (Bull. Office Internat. d'Hyg. Publique, 1940, 32:748). However, due to the fact that preventive inoculation is not in common practice the incidence of tetanus is still very great. The average incidence of tetanus in the U. S. A. from 1947-1952 was 546 cases per year (Hampton, '54) and in South Africa during the period of 1945-1950, 1019 fatal cases were recorded. The annual death rate per million persons (1946-48) was 16.1 (Slome, '54). A total of 237 deaths were recorded in Melbourne during twenty years representing a mortality of 50% of clinical cases. There was no case which could be shown to have occurred after a prophylactic injection of antitetanus serum (Melbourne Pediatric Society, '53). It is evident from these few records that the high mortality and frequent occurrence of tetanus in cases without any prophylactic treatment form a great medical problem which can be solved by obligatory prophylaxis and improved treatment.

The distribution of tetanus bacillus is broad. It has been isolated from superficial layers of cultivated earth (Nicolaier, 1884), from animal (Fildes, '25) and human feces (Tulloch, '19). Also, there are frequent reports that tetanus may be a secondary infection caused by materials in an unsterile condition, e. g. plaster bandages (Murray and Danton, '49), catgut (Savolainen, '50), following tonsillectomy (Bajog, '53) and otitis media (Dave, '53). *Tetanus neonatarum*, following umbilical infection, may occur.

It was revealed by the experiments of Sherrington ('17) and others that there is present a great variability in susceptibility to tetanus toxin in man and in animals. The most susceptible mam-

mals are the horse, guinea pig, monkey and mouse and the most resistant the cat and dog (Fildes, '29a). Simic and Sahovic ('50) found that cancerogenic tissue can also bind the tetanus toxin. The sensitive cells have at least two binding groups. Aristovsky, Kambrova and Firsova ('38) found that dogs are more sensitive than mice to certain types of tetanus toxin. Haku ('39) performed experiments on cold-blooded animals which normally are refractive to tetanus toxin. He concludes that under higher temperatures a third active component is present in the toxin (in addition to tetanospasmin and tetanolysin) which acts upon the ganglion cells of the heart.

Usually an incubation period intervenes between the inoculation or entry of the infectious agent under the skin and appearance of symptoms. The incubation period cannot be reduced to less than eight hours with the usual toxic filtrate. Beyond that point the incubation period is inversely related to the amount of toxin injected (Burrows, '50). The usual incubation period in humans varies from 3-21 days (Bruce, '20). Pillemer and Wartman ('47) produced tetanus symptoms in 30 minutes and death in an hour by injecting 500,000 MLD of crystalline toxin intramuscularly. Pelloja ('50) concludes that the incubation period represents the time required for the toxin to penetrate the neurons and the moment of death does not depend solely on the action of the toxin but also on factors such as the somatic constitution of the animal and the decomposition of the toxin. Meyer and Ransom ('03) relate the incubation period to the distance the toxin has to travel along the nerves to reach the central nervous system. (For further discussion on the incubation period see Imbriano, '50d and D'Antona, '51.)

B. Histopathology

Although pathologic changes occur in tetanus, it is generally agreed that there is no set pattern of changes characteristic of the disease. Most of the pathologic alterations reported in humans are probably postmortem changes. Hassin ('48) emphasizes the importance of differentiating the changes produced experimentally in animals from those occurring in humans. Lesions in the ventral horn cells were demonstrated by Nissl (1896). In a review Barker ('01) pointed out the close resemblance between the changes produced by strychnine and those due to tetanus poisoning. Goldscheider and Flatau (1898) and Chantemesse and Marinesco (1898) observed in their experimental animals gradual alterations

in the nucleolus and tigroid substance resulting in deformity of nucleolus and complete chromatolysis from 2 to 24 hours after injection of the toxin. Claude (1897) and Hassin ('48) reported demyelination associated with round cell infiltration, proliferation of glia and preservation of axons. Recently Zaffiro ('50) observed in guinea pigs that all the organs appeared grossly to be markedly congested. There were small hemorrhages in the lungs, liver and kidneys with areas of necrosis in the liver. Microscopically, the brain showed vascular congestion, edema, proliferation of astrocytes and neuronophagia. In the spinal cord there was congestion, degeneration of motor neurons and neuronophagia. The alterations in humans are similar to those found in experimental animals.

Curling (1936) stated that, "There are, therefore, no morbid changes peculiar to tetanus, and by which it can be recognized." Alterations in the anterior horn cells, medulla, and cortex were reported by Halban ('00) and others. Baker ('42, '49) pointed out that in man the brain is negative or reveals only scattered areas of subarachnoid bleeding and intracerebral petechiae. Prior to the third day no microscopic lesions were present. From the third to the seventh day of illness neuronal changes appear involving scattered cortical areas as well as specific cranial nerve nuclei. Neurons are swollen and show a characteristic perinuclear chromatolysis. From the seventh to the tenth day there appear focal areas of perivascular demyelination. If the patient survives beyond the tenth day the glia proliferates to form scattered foci of small and large glial nodules. All histologic lesions seem to have a vascular distribution suggesting a hematogenous spread of the toxin. Kassay and Máthé ('51) detected changes in the spinal cord, the nuclei of the extrapyramidal tracts, the mesencephalic nucleus of the trigeminal nerve, the hypothalamus and the pituitary gland. They consider that these changes are a result of reflex irritation due to an excess of acetylcholine, and that they represent a hyperfunction leading to the death of the neurons concerned. Wechsler ('52) pointed out that there are no consistent pathologic changes and Courville ('53) states that there are no characteristic sites of inflammation. With the exception of a general or moderate congestion in organs other than the central nervous system, no pathological changes are observed (Zinsser and Bayne-Jones, 1939).

Ranson and associates ('26-'29) made histological observations of muscles which were altered to irreversible gel due to the action of tetanus. Ranson and Sams ('28) studied the action of tetanus

upon muscles with regard to myostatic contracture of Moll (1886). The hypertonus in local tetanus is reflex in character and later the myostatic contracture is superimposed upon it. (Similar conclusions were reached by Klensch and Schlömer ('52) and others.) After prolonged involvement of the muscles mild changes such as an increase in the number of sarcolemmal nuclei and obscurity of the cross-striations were observed. According to the authors the rigidity was related to a change in contractility of the elastic elements in the muscle fibers resulting in shortening the muscles' resting length by 10 to 40 percent. Adams, Denny-Brown and Pearson ('53) were not convinced that the changes are necessarily in the muscle fibers, and believe that a similar phenomenon is common to all true elastic tissue. They feel the uneven intensity of staining and the obscure and irregular striations reported by Davenport, Ranson and Stevens ('29) fall within the limits of variability inherent in the process of fixation. Lesions similar to Zenker's hyaline degeneration have been less often observed and muscle rupture may occur from violent contraction in severe tetanus.

Tetanolysin causes destruction of red blood corpuscles. The endotoxin does not have a specific action or result in a characteristic alteration which differs from the general picture of endotoxin intoxication following administration of a lethal dose. The usual alterations are damaged blood vessels resulting in degenerative changes in the tissues supplied (Burrows, '50).

C. The Spread of Tetanus Toxin

Gumprecht (1893, 1895a, b) states that the first authors who turned their attention to the problem of the spread of tetanus toxin were von Brunner (1891-94) in German literature and Autokratow (1892) and Courmont and Doyon (1892-93-99) in French literature. Brunner's experiments in 1894 were a confirmation and broadening of results observed by Autokratow (1892), Courmont and Doyon (1892) and Buschke and Oergel (1893), however, no sound conclusions were drawn. In accordance with the attitude prevailing at that time, their experiments were interpreted as providing experimental evidence that tetanus toxin was carried from the periphery to susceptible centers in the central nervous system by some component of peripheral nerve trunks.

It was not until Marie (1897), Marie and Morax ('02-'03), Meyer ('01), Meyer and Ransom ('03), Loewi and Meyer ('08), Fröhlich and Meyer ('16) and others performed a series of classical experiments that the first concrete theory was formulated. This theory

later became modified but essentially remained unaltered. According to the theory of Meyer and Ransom ('03) the following events take place in tetanus. From the site of inoculation or natural infection the toxin spreads through the tissue spaces. Some of it may be absorbed directly by the naked terminals of motor nerves, however, Meyer and Ransom believe most of it is absorbed by the lymphatic capillaries and circulated throughout the body by the vascular stream. In this manner the toxin reaches all motor nerve terminals through which it is absorbed. Then it is probably carried in axis cylinders of the motor nerves to the spinal cord where it is fixed by the motor neurons of the anterior horns. After a certain amount of toxin has entered these ganglion cells there is induced a state of increased irritability in these cells and this in turn causes contraction of muscles innervated by these respective cells (homolateral contraction). Excess toxin courses along the fibers of the anterior commissure to the neurons of the other side of the spinal cord producing tetanic contraction of the opposite extremity. After enough toxin has accumulated in the spinal cord via carriage of the toxin from the periphery in the motor nerve trunks, the toxin is fixed by the tactile apparatus of the reflex arc resulting in an increase in the reflexes of the involved extremity. Through further spread of the nonfixed toxin in the direction of the brain new motor centers and reflex arcs are affected.

Recently D'Antona ('49-'51) summed up the fundamental concepts of the above described theory. Among others D'Antona suggests that the motor nerves absorb the tetanus toxin at the motor end plates which are covered only by the delicate sheath of Henle (neurilemma). The myelin sheath, the membrane of Schwann and the endoneural membrane of Ruffini are absent at this point. The sensory nerves do not absorb the toxin since they frequently terminate in corpuscles (Golgi, Meissner, Pacinian etc.) which are formed by structures impermeable to tetanus toxin or have a biochemical constitution unadapted to fix the toxin. However, Zironi ('51) points to the fact that many motor endings are covered with a neurilemma as they penetrate the sarcoplasm in muscle fibers, and also there are a large number of free sensory endings that do not possess myelin sheaths.

Meyer and Ransom ('03) produced *tetanus dolorosus* by injecting the tetanus toxin into the spinal sensory areas. This never occurred when the toxin was injected peripheral to the dorsal root ganglion. To many workers these results suggested that tetanus toxin does

not pass beyond the dorsal root ganglion (Fletcher, '03 and Teale and Embleton, '19-'20). Firor and Jonas ('38) produced reflex tetanus by intraspinal injections without producing *tetanus dolorosus* or muscular rigidity in the periphery. Zironi ('51) points out that pain analogous to that occurring in *tetanus dolorosus* results from sectioning sacral nerve roots independent of the introduction of toxin. Meyer and Ransom ('03) suggested that tetanus toxin ascends along sensory fibers but much slower than in the motor nerves. Wright, G. P. ('53) explains the slow movement along sensory nerves as due to the lack of a sufficient peripheral pressure gradient in subcutaneous tissue fluid to propel the toxin along sensory-cutaneous nerves to the central nervous system. On the other hand the pressure gradient in muscles is considerably higher as pointed out in Panomarew's experiments in 1928. This agrees with the observations of Meyer and Ransom ('03), Zupnik ('05), Sawamura ('09), D'Antona ('49-'52) and others who observed that descending or general tetanus, but no local symptoms, resulted from injections in sensory nerves, skin, testicles, etc.

In the years following Meyer and Ransom's ('03) experiments numerous investigators presented evidence supporting their neural theory: Permin ('14), Friedemann et al ('39-'49), Buzello ('29), Doerr et al ('35, '36), Bromeis ('38), Roofe ('47, '48), D'Antona ('49-'52), Zaffiro and Edoardo ('50) and others. The theory was also accepted by numerous clinicians (Jelliffe and White, '17; Wechsler, '52 and others).

Although the above authors presented experimental evidence for a theory which postulates a centripetal flow of axoplasm or some other means by which substances are carried centrally along the axons, not all results of work related to the structure of the axon support such a theory. For further discussion on the structural aspects of the problem see review articles of Parker ('29), De Renyi ('32) and the more recent electron microscopic observations of De Robertis ('54), Meyer ('55) and Young ('56).

The Marie-Meyer central neural theory became a subject of controversy shortly after its formulation. According to some authors it failed to account in a satisfactory manner for many of the features of the disease (Abel and Hampil, '35). New theories and modifications were proposed. The variations of Marie-Meyer theory are, (a) the carriage of toxin in the lymphatic vessels of the peripheral nerves to the cerebrospinal fluid, thus affecting the centers in the central nervous system, and (b) the tissue space theory which

proposes a centripetal movement of the toxin in perineural spaces of peripheral nerve trunks toward the spinal cord and a continuous upward movement in the cord to the vital centers in the medulla oblongata.

The lymphatic spread of tetanus toxin in the peripheral nerve trunks towards the spinal cord and cerebrospinal fluid was first suggested by Gumprecht (1895 a, b). Field ('06-'07) was of the opinion that tetanus toxin does not travel up the nerve by reason of specific attraction to nervous tissues, but because the lymphatic flow in the nerve is from the periphery towards the center. Teale and Embleton ('20) strongly supported this theory although they did not exclude the possibility of axonal carriage. Golla ('17) also believed in some degree in the perineural lymphatic spread. Partial involvement was proposed by many others (Stinzing, 1893, and Robertson, '16). Wischnewsky ('28) traced methylene blue centrally in nerve trunks and Horster and Whitman ('31) detected dye in the cerebrospinal fluid following injection of trypan blue and tetanus toxin intraneurally. These results were interpreted as further support for the theory that tetanus toxin is carried to the central nervous system via the lymphatics of peripheral nerves.

The tissue space theory was first formulated by Panomarew ('28) and his associates. These authors demonstrated a direct connection between the perineural tissue spaces and subarachnoid spaces. They noticed that the rate of centripetal movement of the toxin along the nerve trunk is dependent on the subarachnoid pressure gradient in cerebrospinal fluid and on the pressure in muscles in the periphery. Abel, Evans, Hampil and Lee ('35) pointed out that the tissue pressure of muscles is not of sufficient magnitude to move solutions through narrow tissue spaces and to overcome the pressure in the cerebrospinal fluid. Abel's ('34) measurements of such a pressure were recently criticized by Wright, G. P. ('53). Wright along with Drinker and Field ('33) and Barcroft and Dornhorst ('48) point out that during the mildest exercise, such as walking, an adequate pressure gradient is produced several times a minute. Wright, E. A., Wright, G. P., Baylis, Ambache, Davies and their associates ('48-'54) attempted to disprove the axis cylinder as a means of transportation of tetanus toxin. In a series of experiments they present strong evidence demonstrating centripetal movement of toxin in perineural tissue spaces of peripheral nerve trunks and the spinal cord.

Indirect support was given to the endoneural and perineural lym-

phatic spread or tissue space spread theories by the anatomical findings of Key and Retzius (1875), Funaoka and Yamada ('29), Clark ('29), Mantell ('32), Sullivan and Mortensen ('34), French, Strain and Jones ('48), Brierley and Field ('49), Moore ('53), Moore, Hain, Ward and Bridenbaugh ('54) and others. These authors used intraneural or intrathecal injections of dye, radiopaque materials, radioactive phosphorus, drugs and other substances, and detected its appearance in cerebrospinal fluid or along the peripheral nerve trunks.

Others argue that the many substances and techniques used for the above studies actually dissect a connection between the cerebrospinal fluid and the peripheral nerve. Following an extensive review of the literature Elman ('23) concluded a communication did not exist.

Following injection of tinted radiopaque media into a peripheral nerve, French, Strain and Jones ('48) reported free flow of the medium within the fasciculi, however, lateral diffusion was prevented by the endoneurial connective tissue planes. In the distal portion of the nerve the medium was confined to the periaxonal connective tissue. Adjacent to the dura it assumed a position in the perineurial interstices and finally in the perineurium itself. From this position the medium entered the subdural space and finally broke through into the subarachnoid space at or near the arachnoid cuff.

Moore ('53) followed the course of colored efocaine in the peripheral nerve. The material remained in the epineurium and entered the parenchyma of the spinal cord directly. The dorsal root ganglion acted as a temporary block to the central flow of the medium. After passing up and down in the spinal cord, some material diffused through the pia to enter the subarachnoid space. Elman ('23) reported that although intravital injections of India ink introduced into cerebrospinal fluid escaped from the cord into lymphatic channels of the region, he could not demonstrate the existence of a fluid pathway physiologically connecting subarachnoid cavity with perineural spaces. Weed ('14-'15), Iwanow and Romodanowsky ('27), Zhdanow ('31), Kurdümov ('32) and Defrise ('30) pointed out that there is no direct connection between perineural and interfascicular lymph vessels and the central nervous system and cerebrospinal fluid, but that lymph from peripheral nerve trunks reaches lymph nodes adjacent to the vertebral column and eventually the principal lymphatic vessels. Similar conclusions were drawn

by Abel, Evans, Hampil and Lee ('35), Abel, Hampil and Jonas ('35) and others.

Although it is commonly accepted that epineural lymphatics do not communicate with the cerebrospinal fluid it is interesting to note the experiments of Brierley and Field ('48) and Field and Brierley ('48). These authors found that finely divided India ink particles injected into the subarachnoid space may be traced along emerging nerve roots to the prevertebral lymphatics. The flow is dependent on the pressure gradient between the subarachnoid space and abdominal lymphatics. The flow can be reversed by increasing pressure in the abdominal lymphatics to 15 mm Hg.

Causey ('48) applied pressure to nerve trunks and subsequently measured the fibers and nerve trunk diameter. He concluded that perineural tissue spaces filled with tissue fluid actually exist. Birren and Wall ('56) studied the proportion of nerve fibers, connective tissue spaces, and blood vessels in the sciatic nerve of the rat, preparing the tissue by the freezing-drying method. They found in animals of 50-250 days of age the median volume of the nerve occupied by nerve fibers was 60.9 percent, the connective tissue spaces amounted to 36.8 percent and blood vessels 1.2 percent.

The following arguments have been presented by various authors in support of the general concept that tetanus toxin reaches the central nervous system through peripheral nerve trunks:

1. To the present time numerous investigators (Baylis, *et al*, '52; Wright, *et al*, '51) have demonstrated the presence of toxin in nerves nearest the point of inoculation. Meyer and Ransom ('03) detected toxin in the nerve one and one-half hours after subcutaneous injection. Furthermore, Riggs and Matzke (unpublished) by utilizing a fluorescent antibody technique showed that the toxin reaches the sciatic nerve within six hours following inoculation into the gastrocnemius muscle of the rat.

2. If antitoxin is injected into the nerve trunk or spinal cord segment proximal to the point of inoculation of the toxin, tetanus fails to develop in that extremity (Meyer and Ransom '03; Permin, '14; Teale and Embleton, '19-'20; Roofe, '47 and others). Antitoxin injected into the sciatic nerve of the left leg delays or prevents the onset of tetanus in the right leg into which toxin was inoculated (Wright, *et al*, '51).

3. Various blocking agents have been introduced into the sciatic nerve in an attempt to prevent the spread of toxin. Teale and Embleton ('19-'20) using tincture of iodine, egg albumin and horse

serum successfully delayed the onset of symptoms. Wright *et al* ('51) and Baylis, Mackintosh, Morgan and Wright, G. P. ('52) injected ethanolamine oleate and quinine urethane into the sciatic nerve. These materials had the effect of stimulating the deposition of connective tissue without interfering with the function of the axons. The severity of the symptoms resulting from injection of toxin distal to the sclerosed area was greatly reduced.

4. Following intraneural injections a wide variety of materials have been traced along peripheral nerves to the central nervous system by a number of techniques. Recently Brierley and Field ('49) with India ink and Wright *et al* ('51) with radioactive materials claim that some element of the peripheral nerve constituted the pathway to the central nervous system for these various materials. Perdran ('37) suggested the axis-cylinder as a pathway for dyes and salts in solution. Marinesco and Draganesco ('23) felt that the tissue spaces of peripheral nerves constituted the pathway for herpes virus, whereas Howe and Bodian ('42) felt that the axis-cylinders constituted the route to the central nervous system for the virus of poliomyelitis. All of these experiments indicate some element of the peripheral nerve is involved, however, there is no agreement as to whether this may be the axis-cylinder, the tissue spaces or lymphatics.

5. Results of experiments where the peripheral nerves or spinal cord were transected also indicate that the peripheral nerve serves as a pathway for the toxin to the central nervous system. Meyer and Ransom ('03), Permin ('14), Firor, Lamont and Shumacker ('40), Friedemann *et al* ('41), Baylis, Joseph, Mackintosh, Morgan and Wright, G. P. ('52) and others were able to avert fatal intoxication if the spinal cord was sectioned at a site between the point of inoculation and the brain stem. By sectioning the peripheral nerve von Brunner (1894), Courmont and Doyon (1899), Tizzoni and Cattani (1890), Ranson ('28) and others, were able to prevent the development of tetanus in the muscle innervated by that nerve. By freezing a segment of the sciatic nerve and allowing 16 days for recovery of the blood supply and connective tissue Roofe ('47, '48) was able to prevent the development of local tetanus. Zaffiro and Edoardo ('50) prevented the development of local tetanus and markedly delayed the onset of symptoms of general tetanus by longitudinally sectioning the peripheral nerve trunk.

6. Meyer and Ransom ('03) injected toxin directly into the spinal cord. The first musculature involved was that innervated by nerves

arising from the injected segment. Sawamura ('09) observed tetanic involvement of the muscles in the leg opposite to that which was injected with toxin. Wright, E. A. *et al* ('51) was able to trace radioactive materials and tetanus toxin into the nerve of the leg opposite to the injected extremity and also up the spinal cord to the brain stem. In other experiments these authors ('50) were able to bring about salivation, strabismus, torticollis and bradycardia following injection of the toxin into cranial nerves VII, X, XII. Although the peripheral structures involved are widely separated anatomically, they all receive their motor innervation from nuclei which are in proximity, one to another, in the brain stem. Furthermore, electromyograms indicate that the muscles which are first and most severely involved are those innervated by the spinal cord segment innervating the inoculated area and not necessarily those muscles which are adjacent to this area (Davies *et al* '54). Rocchi ('40) observed a markedly increased electrical sensitivity in muscles injected with toxin and showing tetanic symptoms as compared with the rest of the musculature in the body.

7. Meyer and Ransom ('03) suggested a hematoencephalic barrier existed for tetanus toxin. This theory has been supported by the extensive work of Friedemann and associates (Zuger, Hollander and Tarlow, '39-'41). These authors were able to demonstrate both local and general tetanus following intramuscular inoculations even though all circulating toxin was neutralized by an antitoxin. Local tetanus was produced in actively and passively immunized animals following intramuscular injection of toxin (Meyer and Ransom, '03 and Permin, '14).

8. Firor, Lamont and Shumacker ('40) and Wright, E. A. ('53) demonstrated that the lethal dose of toxin decreases progressively and steeply when inoculations are made into the blood stream, limb musculature, nerve trunks, spinal cord, and medulla oblongata respectively.

9. Bromeis ('38) correlated the toxin content of a nerve at different levels with the time of inoculation. Permin ('14) injected toxin intramuscularly in the hind leg, antitoxin in the blood and cut the nerve after the injection at different times. Tetanus was not prevented if the nerve was cut five hours after injection. From that he concluded that tetanus toxin spreads along nerve fibers rather rapidly. On the basis of time of toxin application and time of onset of tetanus symptoms, Roofe ('47) determined that the toxin travels along the sciatic nerve at the rate of 3.35 mm/hour.

Descombey and Robin ('30) pointed out the importance of the site of inoculation to the time of development of the symptoms. The closer the site of inoculation is to the central nervous system, the shorter the distance the toxin needs to travel and thus, the shorter the incubation period.

10. Friedemann, Hollander and Tarlov ('41) and D'Antona ('49a, b, '51) point out that it takes 20 to 80 times more antitoxin to neutralize intramuscularly injected toxin than to neutralize the same amount injected intravenously. If, following intramuscular injection of toxin, the nerves supplying that extremity are sectioned the amount of antitoxin necessary to neutralize this toxin is the same as that required to neutralize the same amount of intravenously injected toxin (Friedemann, Zuger and Hollander, '39b and D'Antona, '49a, b, '51). Friedemann and Traub ('49) pointed out that the quantity of antitoxin needed to save an animal inoculated subcutaneously with tetanus toxin is considerably reduced if the antitoxin is introduced into the spinal cord rather than into a vein.

11. The use of parabiotic animals in studying the spread of tetanus toxin was first suggested by von Sauerbruch and Heyde in 1908. Ranzi and Ehrlich ('09) injected toxin into one member of a pair 5 days after they were placed in parabiosis and noted that the uninjected parabiont failed to develop any symptoms of tetanus. Rocchi ('40) utilized the technique of crossed sciatic nerve regeneration in parabiotic rats. In one pair with 20 days regeneration time toxin was injected into the extremity into which the sciatic nerve was regenerating from the opposite animal. Tetanus developed in the opposite animal presumably by coursing along the crossed regenerated nerve. Eight hours after inoculation of this animal toxin could be detected in the blood and certain organs of the uninjected animal. Richter and Schreckenbach ('54) produced general tetanus in both parabionts united for 126 days by injecting toxin intravenously in only one. Utilizing a larger series of parabiotic animals, some with and others without nerve cross, Matzke and Fedinec ('55) concluded that toxin will travel rapidly along nerve trunks, however, it may also be disseminated by the blood. These findings that toxin may spread by both the peripheral nerves and vascular stream support those of von Brunner, 1894 and Albert, '18.

A number of investigators deny the importance of the peripheral nerve in the transport of tetanus toxin to the central nervous system

(Zupnik, '00-'08; Albert, '18). In a series of nine papers between 1934 and 1938 Abel and his associates put forth a number of arguments and experimental results supporting the theory that the vascular stream is the main route for the toxin. This theory is supported by a number of other workers particularly Zironi ('51) and Penitschka ('53). The principal arguments cited to support this theory are as follows:

1. Zironi ('51) points out that if the toxin travels by way of the nerve it should then be possible to detect it within the nerve, however, if a nerve from an animal infected with the toxin is homogenized and the homogenate injected into another animal, the injected animal fails to develop tetanus. He therefore concluded that the toxin was not present in the nerve.

It has been demonstrated numerous times that tetanus toxin has a strong affinity for nervous tissue. Despite this fact homogenates of brains of animals infected with toxin did not produce tetanus when injected into other animals (Wassermann and Takaki, 1898). Imbriano ('50c) demonstrated a strong lecithinase activity of the toxin. Riggs and Matzke (unpublished) were able to demonstrate the presence of the toxin in the myelin sheaths of peripheral nerves utilizing a fluorescent antibody technique. This latter may explain the findings of Pochhammer ('09) who suggested that toxin causes local alterations in the myelin sheaths. All of these experiments would indicate that toxin has a strong affinity for nervous tissue and is probably bound by this tissue. In this state it is unable to infect other animals.

2. It is generally agreed by most supporters of the nerve transport theory that the toxin travels more rapidly along motor nerves than sensory. Zironi ('51) argues that the termination of motor fibers are well protected by Henle's membrane and the sarcolemma. This constitutes a barrier as great as that around the free sensory endings, therefore, the toxin should penetrate both equally well. Wright, G. P. ('53) argues that the more rapid movement of toxin along motor fibers is not dependent entirely upon the protection at the motor end plates but upon a pressure gradient between the periphery, namely the muscles, and the central nervous system. This pressure gradient is not as great along sensory nerves.

3. Vaillard and Vincent (1891) and Zupnik (1900-'08) showed that local tetanus may be entirely avoided if the toxin is injected into the subcutaneous tissues of the tip of the toe, the end of the tail, the dorsum of the foot or in the neighborhood of certain joints that

are not in contact with the body of a muscle. These authors felt that this supports the blood dissemination theory and local action on muscles directly. This opinion differs markedly from conclusions drawn from similar experiments by Meyer and Ransom ('03), D'Antona ('49-'52), Wright, E. A. *et al* ('51) and Wright, G. P. ('53).

4. As cited above, if a peripheral nerve is sectioned and the toxin injected distal to this point, the animal fails to develop tetanus. Zironi ('51) feels that this is due to the trophic effect of the sectioned nerves on the peripheral tissues altering the permeability of the vessels and the diameter of the lumen. The toxin, therefore, does not penetrate the vessels as readily as in an animal with an intact nerve. Ranson ('28) observed the development of tetanus following section of the sensory fibers only, indicating that the trophic effects had no influence on the spread of the toxin.

5. Lenormant, Lanari and Devoto, and Pelloja ('51), (quoted by Zironi, '51) sectioned the motor nerve to a muscle in tetanus and noted that the local tetanus did not disappear. Ranson and Sams ('28) believe that local tetanus is first reflex in character and later myostatic contracture is superimposed upon it. Klensch and Schlömer ('52) essentially agree with this conclusion stating there are two phases in local tetanus: a.) the phase of typical tetanus when the muscle contraction is due to an increased discharge of impulses reaching the muscle; and b.) a phase of prolonged contracture due to changes within the muscle itself. This latter phase is not altered by sectioning of the motor nerve to the muscle.

6. Harvey ('39) has shown that if tetanus toxin is injected intraneurally soon after the nerve has been cut, local tetanus appears. He further states that local tetanus cannot be produced after the motor end plates have degenerated. No other workers have been able to repeat his experiments.

7. Abel *et al* ('35) failed to prevent the development of local tetanus by injecting antitoxin into the nerve proximal to the site of inoculation of toxin. Furthermore, they were unable to produce local tetanus by intraneural injections of tetanus toxin. This work is supported by that of Penitschka ('53). He injected $\frac{1}{500}$ MLD of tetanus toxin intraneurally in the hind leg of a dog and $\frac{1}{100}$ MLD intramuscularly into the front leg. Local tetanus appeared in the front leg several weeks before its appearance in the hind leg. This was despite the fact that a larger dosage was injected intraneurally in the hind leg.

No workers have been able to repeat the experiments of Abel and his associates. Most of them have been able to block the course of toxin in the nerve with intrasciatic injection of antitoxin. D'Antona ('51) feels that toxin is absorbed at the motor end plates and passes to the central nervous system more rapidly than when it is injected directly into the nerve trunk. This suggests an explanation of Penitschka's results, namely that the intramuscular injection was more effective.

8. Zironi ('51) believes that antitoxin injected into the vascular stream is less effective because it is diluted and thus there is less chance for it to combine with the specific antigen. Injections into the cerebrospinal fluid are thus more effective since the toxin upon passing through the blood-brain barrier is immediately neutralized by the antitoxin. Many experiments were performed to ascertain which method of antitoxin administration is the most effective. The intravenous and intraspinal are commonly believed to be the most desirable. D'Antona ('51) suggests that toxin or antitoxin injected into the cerebrospinal fluid is absorbed into blood and is transported to peripheral nerves which represent the port of entry for the toxin.

From the above discussion it is evident that a commonly accepted theory as to the mode of transport of tetanus toxin is lacking. Much of the work already done must be repeated and supplemented with results obtained by utilizing new and more refined techniques.

D. The Site and Mode of Action of Tetanus Toxin

It is generally agreed that tetanus toxin attacks neurons of the central nervous system, however, there is considerable disagreement as to the site and mode of action of the toxin in local and general tetanus. The difficulty is due principally to the failure to reach universal agreement as to the route the toxin takes from the site of injection or infection to the susceptible organs. Since there is no generally accepted theory as to the mode of spread of tetanus toxin it is not surprising that there is no universal agreement as to the action of tetanus toxin.

Concerning the mode of action of tetanus toxin, Courmont and Doyon suggested as early as 1893 that the enzymatic action of the toxin resulted in the production of a secondary toxic substance in the muscle. Coltorti and Villari ('54) observed that the enzymatic dephosphorization of ATP (sodium salt) in muscle tissue increased proportionately with the degree of tetanic spasm in the muscle.

They suggested that the spasm was due to nervous stimulation resulting from toxin fixed in the central nervous system. Schulze ('49) found that tetanized muscle produces more lactic acid per unit of tension than does normal muscle, and the solubility of proteins increased in the rigid muscle. Firor, Lamont and Shumacker ('40) and Firor ('47) suggested that a secondary substance was produced in the spinal cord. This substance is either an altered form of tetanus toxin or a new material produced by the action of the toxin on the nervous system. This secondary material is then transported to the vital centers where it has its lethal effect.

Shintaro Asakura and associates ('50) studied the effect of tetanus intoxication on the metabolism of the central nervous system. They were able to recover from the cerebrospinal fluid and blood certain metabolites such as reducing sugars, acetone bodies, pyruvate and alpha-ketoglutarate. This work is interesting in light of the findings of Firor and associates ('40) working with cross-circulated dogs, and the observations of Matzke and Fedinec ('55) on parabiotic rats. The latter injected one parabiont and noticed that the uninjected animal died suddenly without showing any of the typical symptoms of tetanus. Time of death of both animals was approximately the same. Zironi ('51) states that some rabbits injected subcutaneously with toxin die without showing typical symptoms of tetanus. On the other hand, Friedemann, Hollander and Tarlov ('41) deny the production of a secondary substance.

Klemm (1889) suggested that an actual alteration in the molecular configuration of motor nerves resulted in a lowering of the resistance in these nerves to efferent impulses. This in turn brought about an increased contraction of the musculature of the affected side. Pochhammer ('08-'09) suggested that focal alterations in the myelin sheaths of both afferent and efferent fibers of the motor nerve trunk result in "short circuiting." He felt this theory could account for the symptoms of local tetanus. It is interesting to note that by using the fluorescent-antibody technique it can be shown that toxin is present in the myelin sheaths of peripheral nerves and the protoplasm of the nerve cell body (Matzke and Riggs, unpublished.)

Harvey ('39) suggested that tetanus toxin affects the metabolism of acetylcholine and cholinesterase content of the muscles involved. Stevenson ('55) reviewing this problem states that tetanus toxin is irreversibly fixed at cholinergic endings or at a point on the unmyelinated terminal fibrils proximal to the acetylcholine release region. He favors the latter site as the most likely

since the toxin does not appear to depress the acetylation of choline *in vitro*. There is a decrease in the release of acetylcholine which Stevenson feels is secondary to a block in transmission of the impulse proximal to the acetylcholine release region. He further points out that the physiological disturbances resulting from fixation of the toxin in the region resemble those which follow the post-traumatic degeneration of a nerve. The period required for complete recovery in local tetanus is within the range of time required for the repair of a crushed nerve.

Hajek, Godbey and Hines ('47) studied the functional changes in muscle and nerve resulting from prolonged shortening. They observed that the function of a muscle was decreased after tenotomy or tetanus injection. This effect was reversible. In the case of tetanus the normal functional state was re-established 50 days after injection.

Before the discovery of the tetanus bacillus it was commonly held that the seat of action of tetanus was the spinal cord (Curling, 1836). This opinion was held by many of the early writers such as Galen, Fernelius, Willis, Hoffman and Lieutaud (Abel and Hampil, '35). Finally in 1903 Meyer and Ransom formulated a theory which clearly stated that the site of action was the cell bodies within the central nervous system. Heiberg, who wrote in 1861, was one of the earlier writers who felt that the disease involved the blood, resulting in blood poisoning, the effects of which were localized in the muscles.

The fact that both local rigidity and general involvement may be present in tetanus led to the conclusion that the toxin may have a two-fold action, one on the central nervous system and the other on the muscles or motor end plates. This view was supported by Klemm (1889), Veillard and Vincent (1891), von Brunner (1894), Zupnik ('00-'08) and by many later workers. Abel and associates ('34-'38) and Penitschka ('53) support this theory. They feel that the toxin exhibits both a central and a peripheral action each independent of the other. The motor nerve cells of the spinal cord, medulla and pons are attacked by the toxin whereas the unremitting rigidity of voluntary muscles results from the fixation of the toxin by the motor end plates. Zironi ('51) presents a similar view which states that tetanospasmin is fixed by the muscle and this in turn excites the motor and sensory nerves which facilitates the fixation of the circulating toxin by the neurons and the corresponding segments of the spinal cord.

Wright, G. P. ('54) states that although there is general agreement that local tetanus occurs only when the proprioceptive reflex mechanism is intact, the point or points in this reflex pathway which are attacked by the toxin have not yet been determined. He suggests three possible sites of action of the toxin: (1.) the myoneural junction, (2.) the proprioceptive sensory nerve-endings, and (3.) the central synapse.

1. *Myoneural junction.* Harvey ('39) following sectioning of the sciatic nerve, injected tetanus toxin into the tibialis anticus muscle of the cat. He noted that upon applying a single shock to the distal end of the cut nerve repetitive action potentials in the muscle could be recorded. From this he postulated that the tetanus toxin brought about changes at the myoneural junction which had the effect of converting a single excitation into a brief tetanus. Göpfert and Schaefer ('40), Acheson, Ratnoff and Schoenbach ('42) and Perdrup ('46) could not confirm Harvey's findings.

2. *The proprioceptive sensory nerve-endings.* Sherrington ('06) drew attention to the similarities between tetanus and decerebrate rigidity. This led a number of workers to suggest that local tetanus is brought about by pathological exaggeration of the sensitivity of proprioceptive end organs (Liljestrand and Magnus, '19; Ranson, '28; Schaefer, '44; Perdrup, '46). Klensch and Schlömer ('52) believe that to demonstrate local tetanus a central excitation by the toxin and a peripheral nonspecific stimulus is necessary. Vrbova ('54) demonstrated that if the limb of a rat is fixed in an extended position the effects of local tetanus are exaggerated, whereas if the limb is fixed in a flexed position the rate of involvement of tetanus is decreased. She concluded from this that the proprioceptors are important in the development of tetanus.

3. *Spinal cord synapse.* Gumprecht (1893) suggested that tetanus acts on the central nervous system resulting in local rigidity. This is also an important portion of the theory formulated by Meyer and Ransom ('03). Sherrington ('06) observed that the effects of strychnine poisoning are similar to those appearing in tetanus. A large number of workers contributed evidence strengthening this theory that the action of tetanus toxin is on the spinal synapse (Friedemann, Hollander and Tarlov, '41; Friedemann and Traub, '49; Davies, Morgan, Wright, E. A. and Wright, G. P., '54). Vejss and Kozesnik ('54) lowered the body temperature of animals by cooling or by injecting anesthetic drugs such as lobeline and choral hydrate. They noted that the development of tetanus was markedly

hindered. They felt this indicated that the locus of action of tetanus toxin is the central nervous system. Doerr and Seidenberg ('35) injected a sublethal dose of toxin into the lower extremity bringing about a condition of local tetanus. Following this he injected a lethal dose into the upper extremity. He noted that the symptoms of local tetanus in the lower extremity were exaggerated by what he concluded was a flow of impulses from the cervical region of the cord, brought about by complete poisoning of this region by the toxin. He referred to this as his dynamic activation theory. Brooks, Curtis, and Eccles ('55) confirmed the findings of Sherrington that the action of tetanus toxin in the spinal cord closely resembles that of strychnine. They felt that the toxin acts by suppressing all types of synaptic inhibition rather than converting this inhibition to excitation. The symptoms of general tetanus may be similarly explained in that the synaptic inhibitory action is suppressed as the toxin spreads through the central nervous system.

E. Treatment of Tetanus

In clinical literature and textbooks many forms of tetanus are described. Thus we find descriptions of cephalic tetanus, ascending tetanus, descending tetanus, *tetanus neonatarum* in which the organism enters the umbilicus, puerperal tetanus in which the mother is infected during delivery, postoperative tetanus from surgical wounds, and recurrent tetanus in which the symptoms seem to disappear only to recur (Nielsen, '51). Idiopathic or medical tetanus is probably nonexistent as such, but is a form of wound tetanus which develops very late after the original infection has been overlooked or forgotten (Wechsler, '52). Courtois-Suffit and Giroux in 1918 presented a broad description of different forms and variations of tetanus. Generally there are two forms of the disease, the generalized and the localized. The characteristic manifestation of local tetanus is a persistent rigidity of a group of muscles. This state may develop into general tetanus but cases of recovery without further involvement are also reported. The general clinical picture in man usually begins with stiffness of the jaw and neck, difficulty in swallowing, stiffness of the legs or arms, restlessness, irritability, headache and convulsions. Fever or chilliness is occasionally the initial evidence of the disease. Later, trismus develops and the face assumes the characteristic expression, the so-called sardonic smile (*risus sardonicus*). The abdominal and lumbar muscles may assume a completely rigid state. The contraction of the back muscles is often so great that episthotonos occurs. The most char-

acteristic feature of general tetanus is the development of painful convulsions which are elicited by the slightest stimuli. Profuse sweating accompanies the seizures and the viselike contractions of the chest muscles renders the patient unable to cry out. Dysphagia, cyanosis and asphyxia sometimes appear. The pulse and respiratory rates are increased and the temperature commonly rises 2° to 5° F. Death sometimes occurs from spasm of the respiratory muscles. More frequently, however, the immediate cause of death is not apparent (Firor, '47). The basal metabolic rate in tetanus is moderately high and exceeds the normal by 114% (Holmdahl and Thoren, '54). The factors which are important in determining the course of development of the disease are described by Cole ('40) as: age and general physique, sex, type and severity of the wound, site of the wound, incubation period, rate of onset of symptoms, time at which antitoxin is given, and whether or not prophylaxis antitoxin has been given. Similarly Firor ('40) points to these factors as those which can influence the therapeutic result. Cole ('35a) classifies clinical tetanus into four groups: 1) local tetanus, only; 2) generalized rigidity with slight or absent reflex spasm and irritability; 3) generalized rigidity with marked reflex spasm and irritability followed by slowly subsiding generalized rigidity; and 4) marked and continuous spasms with hyperpyrexia and death from cardiac or respiratory failure.

The treatment of tetanus is closely allied with the prevailing theory or theories regarding the etiology of the disease. It seems impossible to present a standard description of treatment due to the immense number of clinical reports which, prior to the discovery of antitoxin, merely recommend an empirical treatment which was based on a meager knowledge of the disease (viz. reports published in Index Cat. of Surg. Gen. Wash. 1893). Even the present day treatment is a matter of controversy dependent on new experimental and clinical evaluations. The fact remains that certain aspects of the etiology of tetanus are still not satisfactorily explained. Chackleton ('54) suggests the following steps in the treatment of tetanus: 1) prevention of the absorption of further toxin by the administration of antitoxin and surgery of the wound; 2) control of reflex spasm; 3) prevention of intercurrent pulmonary infection; 4) control of fluid and electrolyte balance; and 5) maintenance of strength. See Möllerfeld ('55), Smith ('55) and Drew ('54) for review and modern treatment of tetanus.

Treatment with low molecular polyvinylpyrrolidone (Schubert, '54) has been described. Some authors obtained good results with

ACTH (Lewis, Satoscar, Joag, Dave and Patel, '54) whereas others obtained little or no effect (Greene, Ambrus and Gershenfeld, '53). Also the method of artificial hibernation has not yet been standardized (Chesni, '53; Weisse, '55). The more commonly used therapeutic agents for treatment of tetanus are curare, myenesin, penicillin, sedatives and antisera.

The prophylactic value of antisera and the controversy regarding its therapeutic effect and amount and route of administration have already been pointed out. Treatment of the wound has to be conservative. Radical surgical intervention such as amputation (Lanfranchi, 1295; Rose, 1897; Clemmey, 1898; Smith, '05-'06) does not alter the ensuing development of tetanus. (McClintock and Hutchings, '13; Coleman, '30 and Abel and Hampil, '35.) Tracheotomy has been used as early as 1837 by Curling and 1856 by Humphrey. Inasmuch as respiratory complications from spasmodic contraction and respiratory failure are common in severe tetanus (Turner and Galloway, '49) or in oversedation, clinicians still recommend its use (Herzon, Killian and Pearlman, '51 and others).

Eccles, Katz and Kuffler ('41); Eccles and Kuffler ('41); Kuffler ('42a, b, '43) described the action of curare on the myoneural junction as a differential screen, permitting normal impulses to pass while blocking frequencies outside the normal range of duration. McIntyre ('49) presented a broad review on curare; its history, nature and clinical use. According to him Sewell, a veterinarian, first used curare in animal tetanus. According to Drew ('54) Burrall in 1858 was the first to use this drug in human tetanus. Drew also pointed out that the modern management of clinical tetanus with curare began with the work of Florey, Harding and Fildes ('34), Cole ('34), Mitchell ('35) and West ('36). The great value of the aqueous or longer-acting depot form is emphasized by many workers, and different forms of application are described (Cole, '35b; Schlesinger, '46; Deters and Briggs, '52; Siguier et al '54 and others). The danger of curare overdosage is discussed by Foregger ('50) and Pearlstein and Weinglass ('44).

Since Berger and Bradley ('46, '47) introduced it, myenesin has been widely used in the management of tetanus (Diaz-Rivera, Trilla and Pons, '54). A number of theories have been suggested as to its site of action; namely, diencephalon and brain stem (Stephen, '47), brain stem and spinal cord (Schlessinger, Drew and Wood, '48), selective action on subcortical nuclei, cord and myoneural junction progressively (Gammon and Churchil, '49), and subcortical efferent pathways (Finkelman, '49).

Sedation is widely used, mostly in combination with muscle relaxant drugs (McDonald, '49). Antibiotics, especially penicillin, is highly recommended for control of symbiotic organisms. (Diaz-Rivera, Deliz, Berio-Suarez, '48; Diaz-Rivera, Ramirez, Pons and Torregrosa, '51).

F. Summary

1. There is general agreement as to the bacteriological and immunological characteristics of tetanus. However, many questions concerning the chemical structure of the toxin and its action *in vivo* remain to be answered.

2. Pathologic changes resulting from tetanus apparently do not follow a set pattern from individual to individual. This is further complicated by the presence of post-mortem changes in most fatal cases of human tetanus, however, it is apparent that following recovery from a sublethal dose of toxin, no permanent alterations in the central nervous system occur.

3. The treatment of tetanus has been empirical and aimed at reducing the circulating toxin by administering antitoxin, preventing secondary invasion, eliminating muscle spasms and treating the site of infection.

4. Considerable controversy exists over the route followed by the toxin from the site of injection or infection to the central nervous system. There are a number of supporters for each of the following pathways:

- a. the nerve fibers
- b. the perineural tissue spaces
- c. the perineural lymphatics
- d. the vascular stream
- e. a combination of any two or more of the above.

5. Disagreement also exists as to the mode and site of action of the toxin. The following are some of the theories that have been proposed:

- a. Direct action on the central nervous system.
- b. Peripheral action on muscles, motor plates or sensory endings.
- c. Dual action on the periphery and central nervous system.
- d. Acts as an enzyme altering the activity of the cell.
- e. The toxin is transformed or results in the production of a secondary substance which in turn is toxic.

It is apparent from the above discussion that a great deal of experimental work must be done to answer the many questions still

remaining in all phases of the tetanus problem. The objective of the following experiments is to help clarify some of the problems related to the spread of tetanus toxin in the body.

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MATERIALS AND METHODS

Rats from a highly inbred Sprague-Dawley strain were used in all the experiments. An attempt was made to utilize littermates for each experimental group. If this was not possible, animals of approximately the same age and weight were selected. Both sexes were represented in each experimental group. Diet, temperature and other environmental conditions were carefully controlled.

The tetanus toxin utilized in the experiments had a potency of 640,000 MLD/cc and the antitoxin 4,800 American units per cc. Evipal Soluble injected intraperitoneally was used as the anesthetic. Immediately before using, all these substances were diluted with triple distilled water. The toxin and antitoxin were injected intramuscularly, intravenously or intraneurally with a micrometer syringe to which a 30 gauge hypodermic needle was mounted.

Experimental Series I. In order to determine the dosage of toxin necessary to kill fifty percent of the animals injected (LD 50), eight groups of ten animals each were inoculated intramuscularly with equal volumes of the following dilutions of the toxin: 1:300, 1:400, 1:450, 1:475, 1:500, 1:550, 1:575, 1:600. The volume delivered in each case was 0.0015 ml/100 gr. body weight.

Experimental Series II. The relationship of the time and pattern of development of symptoms and time of death to the site of inoculation was studied in three groups of ten animals each. Each animal of the first group received 2 MLD of toxin in the right gastrocnemius muscle. In animals of the second group, the right sciatic nerve was exposed and 2 MLD of toxin was injected peripherally into the nerve. Care was taken to prevent leakage and backflow from the nerve. The procedure was carried out with the aid of a binocular microscope. In animals of the third group 2 MLD of toxin were injected into the right saphenous vein of each.

The vein was exposed and the inoculation observed with a binocular microscope. The type of symptom and time of appearance was recorded as well as the time of death.

Experimental Series III. At 21 days of age the right sciatic nerve was sectioned and resutured in each of 31 rats. From 200 to 375 days were allowed for regeneration. The degree of functional recovery was determined by noting the reaction to nociceptive stimuli and direct electrical stimulation of the sciatic nerve proximal to the suture. If the nerve fiber plays a role in the transport of the toxin, the rate of passage of the toxin along the small regenerated fibers should be slower than that along the normal nerve fibers. Two MLD of toxin were injected into the nerve distal to the suture. The time of appearance of symptoms was noted. The animals were sacrificed and the number of regenerating fibers distal to the suture determined.

Experimental Series IV. To determine whether the number of fibers in the sciatic nerve influenced the rate of passage of the toxin six groups of five animals each were used. Varying numbers of nerve fibers were destroyed with an electro-coagulator. One of the following strengths of current were applied to the sciatic nerves of members of each group for the indicated time: 0.5 mamp, 15 sec; 1 mamp, 10 sec; 1 mamp, 15 sec; 1 mamp, 20 sec; 1 mamp, 25 sec; 1 mamp, 30 sec. Ten days were allowed for regeneration of the connective tissue and blood vessels. Two MLD of toxin were injected into the nerve distal to the lesion. Immediately after death the sciatic nerve was removed and sections distal to the lesion were stained using the silver method of Romanes ('50). The number of intact fibers was compared to that found in the normal left sciatic nerve.

Experimental Series V. The effect of complete destruction of the nerve fibers on the spread of tetanus toxin was studied in 29 rats. The right sciatic nerve was crushed over a distance of 4 mm with a flat forceps. Between one and 100 hours after crushing 2 MLD of toxin were injected into the right sciatic nerve below the crushed area in 14 animals. Eight rats were inoculated at intervals between 100 and 200 hours and 7 between 200 and 300 hours after crushing.

Experimental Series VI. In order to determine the role of the tissue spaces of peripheral nerves in the spread of tetanus toxin 80 rats were divided into seven groups. Five controls were inoculated in the right gastrocnemius with 2 MLD of toxin. Fifteen other controls were inoculated similarly with 2 to 5 MLD 48 hours after the

genitofemoral, obturator, femoral, lateral cutaneous of the thigh, posterior cutaneous of the thigh, and hamstring branches of the sciatic nerves were sectioned.

In twenty animals the above nerves were sectioned and the epineurium removed from the sciatic nerve in the middle of the thigh for a distance of approximately 1 cm. This was accomplished by exposing the nerve and carrying out the following procedure with the aid of the binocular microscope. A shallow circular incision through the epineurium was made with an iridectomy knife. The cut end of the epineurium was secured with a fine forceps, peeled distally for the required distance and dissected away. The following day the sensitivity of the skin in the distribution of the sciatic nerve was tested. Those animals that gave a good response were injected with 2.5 MLD of toxin in the gastrocnemius of the operated side. In another group of ten animals the above procedures were repeated, however, in addition, the perineurium was carefully teased open with a blunt hook.

In another group of fifteen animals the right lower extremity was denervated and a segment of the epineurium removed from the sciatic nerve perineurium and opened as described above. Twenty-four hours later 5 MLD of toxin were injected into the right gastrocnemius muscle. Two hours after this 28.8 times the amount of antitoxin necessary to neutralize the injected toxin was inoculated into the left saphenous vein. Animals which survived this procedure and showed no signs of tetanus were reinjected with 5 MLD of toxin in the sciatic nerve proximal to the area from which the epineurium was removed.

In a group of five animals the right lower extremity was denervated and a segment of the epineurium removed from the sciatic nerve. Five MLD of toxin were injected into the nerve proximal to the bare area and antitoxin into the left saphenous vein. Another group of ten animals was treated similarly except that the epineurium was left intact and the toxin injected into the gastrocnemius muscle. In all the animals of this experiment the time and pattern of development of symptoms were recorded.

RESULTS

Experimental Series I. The results of the first experiment are recorded in Table 1. The data reveal that the least amount of toxin necessary to kill 100 percent of the animals was 0.0015 ml/100 gr. body wt. of the 1:400 dilution. This is referred to as the minimum lethal dosage (MLD). The medium lethal dosage (LD 50) is that

amount of toxin which kills 50 percent of the animals. In this experiment this dosage was found to be 0.0015 ml/100 gr. of body wt. of the 1:475 concentration. The same dosage of the 1:550 dilution failed to kill any of the animals although all developed symptoms of tetanus. This is referred to as the dosage of maximal tolerance (LDO).

Experimental Series II. Following injection of the toxin into the gastrocnemius or sciatic nerve the first symptoms appeared in 18-26 hours. The first sign was that of hypersensitivity of the inoculated extremity which was held in a flexed position to prevent contact with objects. This was gradually replaced by spastic extension at all joints of that extremity. A few hours later the tail became rigid arching toward the side of the involved extremity which was moderately abducted. Within 40-50 hours following injection, lumbar scoliosis toward the affected side appeared. At this time the animal may become extremely hypersensitive responding to the slightest stimulus with convulsive seizures. These seizures may result in injury with blood appearing in the mouth, nostrils, and eyes. The scoliosis disappeared when the opposite extremity became involved. However, pleurothotonos directed ventrally resulting from spasticity of the thoracic musculature appeared at 60 hours. There followed in rapid order, spasticity of the forelimbs, trismus, contraction of the facial musculature, immobility of the vibrissae, and depression of the ears. Death occurred in 68-74 hours following inoculation.

It is apparent from the above description that intramuscular or intraneural injection of toxin results in a progressive involvement of the musculature of the body in a segmental manner. This is referred to as local tetanus which may be either ascending (as in the above case) or descending, depending on the site of injection. This is in contrast to blood-borne tetanus which follows the intravenous injection of toxin.

When 2 MLD of toxin is injected intravenously the first symptoms appeared in 54-62 hours. The first signs involved the facial, masticatory, and some of the axial musculature. A few hours later pleurothotonos appeared due to the spastic contraction of the back and neck muscles. Death occurred in 64-72 hours. At this time the animal may or may not show involvement of the extremities. In contrast to local tetanus the site of intravenous injection had no bearing on the sequence of involvement of muscular groups, however, in both cases there was a definite period of time between injection and appearance of the first symptom. This is referred to as the *latent period*. This period was two to three times longer in blood-borne

tetanus than in local tetanus although the time of death was about the same in both groups. The latent period may be shortened in both groups by increasing the dosage and, in addition, in local tetanus, by injecting closer to the central nervous system. At the time of death in ascending local tetanus, virtually all the musculature of the body was involved; this is referred to as general tetanus. This condition rarely occurs in descending and blood-borne tetanus.

Experimental Series III. The degree of functional nerve fiber recovery, following 200 to 375 days regeneration time, varied considerably; however, all animals responded to nociceptive stimuli and direct stimulation of the regenerated sciatic nerve. The number of regenerating fibers averaged 6,289, the range being from 3,800 to 7,867. This is to be compared with an average of 5,958 and range of 5,302 to 6,564 in the normal intact sciatic nerve. The diameter of the regenerating fibers was less than that of normal axons.

Following intraneural injection of toxin distal to the suture, the animals developed the first symptoms of local tetanus in 30 to 38 hours. These appeared in the injected extremity. Typical ascending tetanus followed; however, the time sequence was considerably longer than in the controls. Death occurred at 116 to 154 hours. There was no correlation between the time of appearance of symptoms and death, on the one hand, and regenerating time and number of fibers, on the other.

Experimental Series IV. When variable numbers of fibers of the sciatic nerve were destroyed by electrocautery, the response to nociceptive stimuli and direct electrical stimulation decreased with an increase in the area of the nerve damaged. Histologic sections of the nerve distal to the lesion revealed that the number of intact fibers varied from 635 to 5,435, however, in no instance did the number of intact fibers approach that found in a normal nerve. Unlike the condition found in regenerating nerves, the diameter and general appearance of the intact fibers was comparable to that of those found in the normal nerve. Another important point of comparison with regenerating nerves is that relatively little connective tissue was deposited at the site of the lesion produced electrically as compared with that found at the suture in regenerating nerves.

When toxin was injected into the sciatic nerve, distal to the lesion, local tetanus appeared in the injected extremity in 22 to 36 hours. Typical ascending tetanus followed with death occurring at 133 to 210 hours. Table 2 indicates there is no relationship between the above time sequence and strength of current used to produce the lesion. Furthermore, there was no correlation between the

number of intact fibers and the time sequence of development of symptoms.

Experimental Series V. The results of this experiment are recorded in Table 3. Histologic sections of the nerve distal to the crushed area revealed only degenerating fibers. Despite this fact, local tetanus appeared in the injected extremity in 23 to 30 hours, following inoculation of the sciatic nerve distal to the crushed area. Ascending tetanus, followed by death, occurred at 175 to 245 hours.

Experimental Series VI. The data from this series are recorded in Table 4. In control animals with an intact sciatic nerve and connective tissue sheaths, intramuscular injection of toxin resulted in local ascending tetanus. When the epineurium is removed from the sciatic nerve and the other nerves to the same extremity cut, blood-borne tetanus resulted in 15 of the 20 animals injected with toxin in the gastrocnemius. The remaining five developed local tetanus. Typical ascending tetanus did not proceed beyond the lumbar segments. At this time blood-borne tetanus was superimposed upon this condition.

If, in addition to removing the epineurium, the perineural septa were teased open, all animals developed blood-borne tetanus following intramuscular injection. In these animals tetanus could be prevented if antitoxin was administered intravenously within two hours after injection of the toxin. Antitoxin did not prevent the occurrence of local tetanus if the epineural sheath was intact or if the toxin was injected into the nerve proximal to the bare area, however, the resulting ascending tetanus was arrested by the time pleurothotonus appeared. The animals survived although spastic contractions of the involved musculature persisted for several months.

In the animals where the epineurium had been removed the response to nociceptive stimuli applied to the area of distribution of the sciatic nerve was normal. Histologic sections through the bare area of the nerve revealed that the great majority of the axons were intact and the epineurium absent.

DISCUSSION

Basing his conclusions on the results of others as well as his own work, D'Antona ('51) formulated a theory on the mode of spread of tetanus toxin. He stated that at the site of injection or production, the toxin is absorbed by both the nerve endings at the motor end plates and the blood capillaries. From the former the toxin passes into the central nervous system via the efferent nerve

fibers. The motor neurons in the segments innervating the inoculated extremity are the first to be attacked by the toxin. This results in spastic contraction of the muscles innervated by these neurons. The toxin then follows axons within the central nervous system to the opposite side as well as up and or down depending on the site of injection. This results in a progressive involvement of neurons of adjacent segments and contraction of the muscles innervated by the corresponding neurons. Death results when the vital centers of the brain stem are reached by the toxin.

From the capillaries the toxin is carried throughout the body in the vascular stream. Naked nerve endings of motor end plates throughout the body absorb the toxin which is then transported to the central nervous system by all somatic efferent fibers. The first musculature to be affected will be that with the shortest efferent fibers. Death results from involvement of the vital centers.

The latent period (the time elapsing between injection and the appearance of the first symptoms) is two to three times longer in blood-borne tetanus than in local tetanus, however, the time of death is approximately the same.

The results of the experiments reported here support many aspects of D'Antona's theory. The time sequence and pattern of appearance of symptoms following intramuscular and intravascular injection of toxin agrees with the above descriptions. Tetanus resulting from intramuscular injection of toxin is referred to as local tetanus, whereas, intravascular administration results in blood-borne tetanus. These results therefore support the hypothesis that the toxin reaches the central nervous system via peripheral nerve trunks.

The principal point of disagreement concerns the element of the peripheral nerve trunk responsible for the transport of the toxin. The results of these experiments do not support D'Antona's axon-transport theory. Toxin reaches the central nervous system when all axons have degenerated and only the connective tissue is intact. In these experiments the intravascular toxin may be eliminated by the intravenous administration of antitoxin. Furthermore, the rate of passage of the toxin to the central nervous system appears to be independent of fiber size or number.

Symptoms of local tetanus can be prevented only when the connective tissue of the epineurium is removed and the perineural septa teased open. In this case blood-borne tetanus results following intramuscular injection of toxin unless antitoxin is administered intravenously.

Baylis *et al* ('52) concluded that the toxin reaches the central nervous system via the tissue spaces of peripheral nerves. Utilizing substances which stimulated the deposition of connective tissue in the nerve thus blocking the tissue spaces, they were able to prevent the appearance of symptoms of local tetanus following injection of toxin into the nerve distal to the sclerosed area. The results of the experiments reported here support this conclusion. The removal of the epineurium removes or opens the tissue spaces so that the toxin is prevented from passing along the nerve. It is absorbed into the vascular stream either at the site of injection or it infiltrates the tissue spaces surrounding the bare area of the nerve and is there absorbed by the blood. Deposition of scar tissue at the site of crushing or suturing a nerve partially blocks the tissue spaces and delays the onset of symptoms of local tetanus.

Abel and his coworkers ('34-'38) concluded that the only way tetanus toxin could reach the central nervous system was directly from the vascular stream. Friedemann and associates ('39a, b, '41) state that the blood-brain barrier is impermeable to the toxin. The results of the experiments reported here do not directly eliminate the vascular stream as an alternate route, however, toxin can reach the central nervous system even though all circulating toxin is neutralized by antitoxin. The pattern of development of symptoms of blood-borne tetanus suggests that the toxin passes in via peripheral nerves since the first muscles involved are those with the shortest axons. Wright, G. P. ('53) also points out that the first musculature involved is the most active. He believes that activity increases the pressure gradient between the periphery and central nervous system and thus the rate of flow of the toxin in the tissue spaces.

Further research is necessary to determine the role of the blood-brain barrier in the passage of tetanus toxin into the central nervous system. Furthermore, the present work points out the necessity of determining more accurately the morphologic relationship of the tissue spaces of the peripheral nerves to the peripheral and central tissue spaces and cerebrospinal fluid chambers. Investigations designed to clarify these relationships are being carried out.

SUMMARY AND CONCLUSIONS

1. The following three forms of tetanus were described:
 - a. Local tetanus: A localized group of muscles are first involved unilaterally. The condition spreads segmentally in a caudal and cephalic direction as well as contralaterally

until death ensues. This form results from intramuscular or intraneural injection of toxin.

- b. Blood-borne tetanus: This condition follows intravascular injection of toxin. The masticatory, facial and mid-line musculature are first involved. Death resulting from respiratory or circulatory collapse occurs before the muscles of the extremities show any signs of tetanus.
 - c. General tetanus: This term is used to describe the condition when all the muscles of the body are involved. It usually appears as the terminal stage of ascending local tetanus. It rarely follows blood-borne or descending local tetanus.
2. The time of appearance of the symptoms of local tetanus is independent of the number or size of the nerve fibers to the extremity injected.
 3. Local tetanus will occur in the absence of nerve fibers to the injected extremity even though toxin in the vascular stream is neutralized by antitoxin.
 4. The symptoms of local tetanus are delayed when scar tissue forms on the nerve as a result of crushing or suturing.
 5. Blood-borne tetanus appears when the connective tissue is removed from the nerve to the injected extremity, however, this can be prevented if antitoxin is administered intravenously.
 6. It is suggested that the only route to the central nervous system for tetanus toxin is by way of the tissue spaces in peripheral nerve trunks.

TABLE 1—Determination of MLD, LD50 and LDO

Number of animals	Dilution of toxin	Number developing symptoms	Number dead in 144 hours
10.....	1:300	10	10
10.....	1:400	10	10
10.....	1:450	10	7
10.....	1:475	10	5
10.....	1:500	10	2
10.....	1:550	10	0
10.....	1:575	10	0
10.....	1:600	10	0

Dosage=0.0015 ml/100 gr. body wt.

TABLE 2—Effect of Destruction of Varying Numbers of Nerve Fibers on the Development of Tetanus

Number of animals	Strength of current in mamp/sec	Regeneration time in days	Time of initial symptoms of local tetanus in hours	Time of death in hours	Number intact fibers
5.....	0.5/15	10	30.33±6.33	149.8±31.4	4,111-5,435
5.....	1/10	10	30.0±4.8	140.8±17.8	2,932-3,805
5.....	1/15	10	30.5±5.0	143.6±18.8	1,265-4,100
5.....	1/20	10	27.5±4.0	173.8±44.6	1,378-2,471
5.....	1/25	10	27.0±5.3	191.3±29.1	635-998
5.....	1/30	10	28.0±3.2	155.4±20.1	800-1,648

Dosage=2 MLD toxin injected intraneurally distal to lesion.

TABLE 3—Effect of Total Destruction of Nerve Fibers on the Development of Tetanus

Number of animals	Time of injection in hours after crushing	Time of initial symptoms of local tetanus in hours	Time of death in hours
14.....	0-100	25.6±2.3	214.9±31.4
8.....	100-200	26.0±2.3	208.4±33.9
7.....	200-300	28.5±2.2	216.9±23.0

Dosage=2 MLD toxin injected intraneurally distal to lesion.

TABLE 4—Effect of the Removal of the Epineurium on the Development of Tetanus

Number of animals	Toxin injection site	Sciatic nerve alone	Epineurium removed from sciatic nerve	Perineural spaces opened	Antitoxin administered intravenously	Time of initial symptoms local tetanus in hours	Time of initial symptoms blood-borne tetanus in hours	Time of death in hours
5.....	M	No	No	No	No	31.2±3.4		95.0±8.0
15.....	M	Yes	No	No	No	26.8±2.3		97.8±11.2
20.....	M	Yes	Yes	No	No	(5) 57.0±2.0	(15) 95.1±8.2	137.6±21.5
10.....	M	Yes	Yes	Yes	No		108.5±11.9	168.6±23.4
15.....	M	Yes	Yes	Yes	Yes			
15.....	N	Yes	Yes	Yes	No	28.0±3.5		132.0±9.2
5.....	N	Yes	Yes	No	Yes	27.8±1.2		
10.....	M	Yes	No	No	Yes	28.8±2.0		

Dosage=2.5 MLD

M=toxin injected into the gastrocnemius muscle.

N=toxin injected into the sciatic nerve proximal to area from which epineurium is removed. The 15 animals in the sixth group are the same as those in the fifth group. Toxin was injected intraneurally 14 days after it was administered intramuscularly.

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The Family Succineidae (Gastropoda: Pulmonata) in Kansas

BY

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ABSTRACT. This study consists of a review of the snails of the Family Succineidae in Kansas. Dissections of the soft parts have been made and used with the shells as a basis for taxonomy. Seven species are recognized. The literature is reviewed.

INTRODUCTION

This study was undertaken in an attempt to determine the kinds and distribution of species of the Family Succineidae (Pulmonata = Gastropoda) occurring within the State of Kansas. Prior to 1954,

at which time this problem was selected, nine species of living succineids had been reported within the State. With two exceptions, the identification of these species was based upon characters of shells, without consideration being given to the soft anatomy of the animals.

Until relatively few years ago, all land snails in North America were treated systematically by considering the details of the shell. Tryon (1866) does not mention the soft anatomy of most species of land snails in his monograph, including the members of the Family Succineidae. Three years later, Binney and Bland (1869: 265) characterized the soft parts of *Succinea* as follows: "Animal resembling the animal of *Helix*, but shorter. Eye-peduncles short, expanded at their base or conic; tentacles very short and small. Respiratory foramen in the mantle, in the angle at the posterior part of the aperture of the shell." In their discussion of the various species of *Succinea* in their monograph, mention of the living animal is made only in connection with *Succinea ovalis* Gould (= *Oxyloma decampi gouldi*) (*op. cit.*). Only a terse description of the external appearance of the animal is included in the characters given for this species.

In many families of snails, the shell seems to be sufficient for accurate diagnosis of the various genera and species. The Family Pupillidae may be cited as an example, for the numerous species, some of which are widely distributed in North America, and elsewhere, are separated satisfactorily by such features as size of the umbilicus of the shell, presence or absence of lamellae in the aperture, number and position of lamellae (if present), and similar characters of the shells (Franzen and Leonard, 1947). In addition, color and markings on the shell and number of whorls present are useful taxonomic tools in many families of land snails.

In the Family Succineidae, the shells are not diagnostic; they are simple, lack ornamentation, lamellae, and other characters useful for purposes of identification. Also, shells vary according to age of the animal and according to the environment. Although *Succinea ovalis* Say is readily identified at all ages by the shell, the shells of the younger animals of some other species are similar enough to create confusion. This confusion, due to similarities of shells, exists between genera, as well as species. Separating young *Quickella vagans* and young *Succinea concordialis*, by characters of their shells, is a perplexing task, especially as these two species are commonly found inhabiting the same locality.

Several workers have observed that accurate identification of almost every species of succineid requires examination of the genitalia, especially of the male organs (Pilsbry, 1948; Lee, 1951a). Because of definite differences in the male genitalia of Succineidae, three genera, *Succinea*, *Oxyloma*, and *Quickella*, are currently recognized in North America; not many years ago, all members of this family were placed in the nominate genus, *Succinea*. The distinguishing features of the three genera are discussed in a later section of this report.

The soft anatomy of members of the Family Succineidae was not utilized for taxonomic purposes to any great extent until Quick (1933) published results of a study of European members of the family. His systematic treatment of the family was based mostly on anatomical characters, particularly of the genitalia.

Using the genitalia of the snails as the basis for his study, Lee (1951a) reduced the number of species of succineids recognized in Michigan from fourteen, which had been described solely on the basis of shells, to three species. Lee reported that the appearance of the shell is too variable to be of taxonomic use in most species of the Family Succineidae in Michigan. The present study tends to support this view, although there are several species of succineids in Kansas that seemingly do not occur in Michigan.

It seems paradoxical that the Family Succineidae has been relatively neglected in North America, for species are numerous in this country. Where succineids occur, they are usually far more numerous in total number than all other snails in the locality. I have visited localities in Kansas where the only limit to the number of succineids collected, perhaps consisting of one or two species, was the time factor and the energy of the collector. As cases in point: at the artesian marsh, 1½ miles south of Muscotah, Atchison County, in July, 1955, the supply of *Oxyloma retusa* was seemingly inexhaustible; roadside ditches along Kansas Highway 7, near Iowa Point, Doniphan County, Kansas, harbored *O. retusa* in incredible numbers in April, 1956; at the University of Kansas Natural History Reservation, several miles northeast of Lawrence, Douglas County, great quantities of *Succinea concordialis* were along South Creek in May, 1956; at any one of a number of localities near Lawrence, such as "Haskell Bottoms," *Quickella vagans* was found to be abundant.

In spite of the abundance of Succineidae, few papers of any significance concerning the family have been published in North America; there is one unpublished doctorate dissertation concerning

this family (Lee, 1951a). Numerous locality records pertaining to various species of the family are found in the literature, but the validity of many of these reports is questionable because, in most instances, identifications were based on the shell. Likewise, certain reports concerning the ecology of succineids must be taken advisedly, because of uncertainties of identification.

The primary objective of my study was to report the species of the Family Succineidae existing in Kansas, on the basis of details of their soft anatomy, especially their genitalia. The shells of some species included in this report are so variable as to be of little taxonomic use; this is especially true of *Quickella vagans*, the shells exhibiting considerable variation over the State.

Investigation has failed to verify the occurrence of *Succinea avara* Say and *S. grosvenori* Lea; *S. avara* has heretofore been considered the most prevalent species of Succineidae in Kansas. Perhaps the most significant finding of my study is the widespread occurrence in Kansas of *Quickella vagans*; its shells have been assigned to one or several species of the genus *Succinea* by previous workers.

Future diligent collecting may reveal the presence of additional species of the Family Succineidae to be added to the list of mollusks of Kansas. Detailed ecological studies of all species will be desirable, for most succineids in the State seem capable of inhabiting more than one distinct kind of habitat. It is hoped that additional attention will be focused upon the Family Succineidae in Kansas and elsewhere in North America.

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I am grateful for guidance and suggestions furnished by Professor A. Byron Leonard; he suggested that I study the Succineidae and accompanied me on several collecting trips. The shells shown in Plate I were photographed by him. Professors E. Raymond Hall and John A. Weir read the manuscript and offered valuable suggestions, as did Thane S. Robinson also. My wife, Virginia, collected many specimens, typed the manuscript and assisted otherwise.

REVIEW OF LITERATURE

In Kansas, living gastropods, in general, have been relatively little studied, considering their abundance in species and in numbers of individuals. The earliest report of species of the Family Succineidae is by Binney and Gray (1885:55); they quote F. W. Cragin and J. B. Quintard on the occurrence of *Succinea lineata* Binney (= *S. grosvenori* Lea) near Topeka, Kansas, and at Silver

Lake Township, Shawnee County. In addition, they listed *S. avara* Say as a "widely distributed species" and *S. haydeni* Binney (= *Oxyloma*) from Silver Lake Township as "rather common." A year later, Call (1886:202) reported *S. obliqua* Say (= *S. ovalis* Say) from Neosho County, Kansas. Hanna (1909:96) in a list of the mollusks of Douglas County, Kansas, reported the occurrence of *S. avara* Say ("not common"), *S. grosvenori* Lea, *S. rusticana* Gould, and *S. stretchiana* Bland. Hanna considered *S. stretchiana* "our common *Succinea*" (*loc. cit.*). In the same number of the *Nautilus* as Hanna's paper, Baker (1909:94) noted the occurrence of *S. avara* from Anthony, Harper County, Kansas.

Nothing further was contributed to the literature concerning the Succineidae in Kansas until 1942, when Franzen and Leonard (1942:339) reported on the mollusks of Kingman County. They listed *S. concordialis* Gould and *S. grosvenori* Lea as occurring within that county. The following year, Alice E. Leonard (1943:240) reported *S. concordialis* and *S. haydeni* (= *Oxyloma*) from Meade County, Kansas. Dorothea Franzen (1944:272), in her paper on mollusks previously unreported from Kansas, mentioned that *Succinea haydeni* (= *Oxyloma*) inhabited the artesian marsh south of Muscotah, in Atchison County, in association with various other gastropods. Two years later, Leonard and Leonard (1946:120) recorded *S. avara* as living "along streams in grass and sedges" in Greenwood County, Kansas. Leonard and Goble (1952:1036) in a paper on the mollusks inhabiting the University of Kansas Natural History Reservation, situated 5½ miles northeast of Lawrence, in Douglas County, reported *S. avara* and *S. concordialis*.

In all of the identifications noted above, succineids were identified only by characteristics of the shells. *S. vaginacontorta* Lee (1951b) and *Quickella wandae* Webb (1953) were described from Kansas and both authors followed the modern procedure of basing their diagnoses on characteristics of the genitalia of the animals. Leonard (1950:23) has discussed the fossil record of various members of the Family Succineidae in Kansas, particularly pertaining to the Pleistocene. He has described one new fossil species, *Oxyloma navarrei* (*loc. cit.*) from Kansas, in deposits of Kansan (Mid-Pleistocene) age.

METHODS

Primary attention has been centered upon the soft anatomy of the animals collected in the course of this study. Living specimens of snails were collected from numerous localities over much of the state of Kansas from April, 1955, until August, 1956. Two

rather extensive collecting trips were made possible by the State Biological Survey of Kansas.

Early in this study, difficulty was encountered in keeping alive snails of certain species until they could be examined in the laboratory. This was especially true of *Oxyloma retusa*. Transporting living snails from the field to the laboratory frequently entailed a high mortality rate, which was partly overcome by placing snails in airtight containers. Undoubtedly, the loss of moisture from perforated jars contributed to the death rate of the animals. As an added precaution, living snails were stored in a refrigerator in the laboratory, which aided considerably in maintaining them until they were examined. The use of a portable ice chest when in the field prevented the great majority of snails from dying; this chest was used successfully on a five day trip over the State in June, 1956.

In the field, snails from a single locality were placed in a container and labeled with a field number, locality, and date. At the same time, pertinent information was entered in a field book on a page bearing the field number, locality, date, and additional information pertaining to ecology, weather conditions, associated species of snails and relative abundance of the snails.

Prior to dissection, snails were killed by immersion in hot water after first allowing the animals to extend themselves on a spoon or section-lifter. The temperature of the water should be at, or near, the boiling point. Seven seconds, or less, in hot water is sufficient to relax the columellar muscle. The animal is then easily removed from its shell by inserting a pin in the foot and gently pulling the animal out.

In the early stages of this study, the snails were dissected in water after removal from the shell. A liquid medium prevents desiccation, and aids immeasurably in differentiating the various internal organs. Later, the technique of dissecting in 70 percent alcohol, suggested by Abdel-Malek (1954:104), was followed. Abdel-Malek reported that "dissection in water was found to be inadvisable because various organs of the snail (*Helisoma trivolvis* Say) . . . and the genitalia particularly tend to absorb considerable water" (*loc. cit.*). Dissected soft parts were preserved for future study in small glass vials containing 70 percent alcohol, bearing a label with the field number, locality, specific name, and date of collection; shells of the snails were placed in cardboard containers, bearing a corresponding label.

Genitalia of representatives of the various species of Succineidae examined in this work have been mounted on slides for a permanent record. For study purposes, storage in alcohol is preferable.

Although not given critical attention in this study, because of their questionable taxonomic use, four measurements of the shells of living specimens were made: greatest length (L), greatest diameter (D), length of aperture (LA), and diameter of aperture (DA). From these four measurements, three ratios are obtained: the ratio of diameter of shell to length of shell (D/L); ratio of length of aperture to length of shell (LA/L) and ratio of diameter of aperture to length of aperture (DA/LA).

Measurements were made to 0.1 mm by means of a vernier caliper. Although these ratios have not been treated statistically, the average ratios obtained from a series of shells may be compared with the average ratios of shells from other series. Certain trends are thus brought to light, which will be discussed in the treatment of the several species. In their present form, nevertheless, these ratios have little taxonomic value, because specimens of different species may yield similar ratios.

The standard reference work used in my study is Vol. 2, part 2, of Pilsbry's classic monograph of *The Land Snails of North America* (1948), in which the anatomy of most known species of North American Succineidae are considered.

The genitalia of the several species were drawn by a technique that conveniently results in correct proportions. Intact reproductive systems were mounted on glass slides and projected on white paper by means of a photographic enlarger; the outlines were traced in ink. This procedure was followed in all cases except that, for technical reasons, the outlines for Figures 4, 7, and 9 were drawn freehand. The jaws, Figures 10a and b, were outlined by means of camera lucida.

CHARACTERISTICS OF THE FAMILY SUCCINEIDAE

The Family Succineidae includes a large group of terrestrial pulmonate snails that are world-wide in distribution. Species are most numerous in North America, southern Asia, and Hawaii (Pilsbry, 1948:772). Because of several distinctive characters, discussed in detail by Pilsbry (*loc. cit.*), the family is not considered to be closely related to any other family of pulmonate gastropods.

Jaw (Fig: 10a, b): Perhaps the most distinctive character, found only in the Family Succineidae, is the large, squarish accessory plate

dorsal to the cutting edge of the jaw, which ordinarily possesses a single median projection on the cutting edge. In several species of *Succinea*, ribs are present on the anterior surface of the jaw, but in Kansas, only *Succinea ovalis* possesses such ribs.

Shell (plate I): The shell, which is similar in general form in all species in Kansas, has been primarily responsible for the present confused state of taxonomy in this family. The shell is simple and lacks distinctive color patterns or ornamentation which might be useful taxonomically. It is thin, transparent, and imperforate. The spire is short, and there are up to four whorls in specimens from Kansas. A characteristic feature of the shell is the relatively large aperture, ranging from 50 percent to over 80 percent of the length of shell.

The color of the shell varies among members of a single population, but in general, is some shade of yellow or brown. The family has long been referred to as "the amber snails" (Lee, 1951b). The color of the shells of any species of the Family Succineidae should not be primarily relied upon in identifying species. Although the shells of *Succinea concordialis* have a ruddy or reddish apex, the same condition has been observed in the shells of other species. Furthermore, the color of the shell often changes after death of the animal.

Genitalia (Figs. 2-9): As noted earlier, the reproductive system furnishes the most accurate means of distinguishing species of Succineidae. The genitalia of all species of this family may be termed simple, in that accessory organs, such as dart sacs, muciparous glands, and flagellae, present in some other families of snails, are lacking in the Succineidae.

The succineids are monoecious, as are most pulmonate gastropods. The male and female reproductive systems open to the outside of the animal through a common genital atrium, which is situated immediately behind the right eyestalk. Since male and female systems join at a common atrium, the intact reproductive system may be removed from the animal with comparative ease. A characteristic feature shared by all species of Succineidae is that the darkly pigmented retractor muscle of the right eyestalk passes between the junction of penis and vagina.

Since detailed anatomical and functional studies of the reproductive organs of Succineidae are not available for most species, it is necessary to resort to interpretations based on studies of snails belonging to other families. The unreliability of such extrapolations is obvious.

The *hermaphrodite gland* (ovotestis) is at the extreme posterior end of the animal and occupies the apex of the shell in the living state. Both ova and sperm are formed in this gland. Hickman (1931:243) studied spermiogenesis in *Succinea ovalis* and discussed this organ in some detail. He characterized the hermaphrodite gland as being composed of many acini "pressed closely together, each opening into an atrium which communicates with the hermaphrodite duct." Hickman (*op. cit.*) referred to *Succinea ovalis* as a "simultaneous hermaphrodite" because male and female germ cells develop at the same time from an indifferent germinal epithelium. The color of the hermaphrodite gland is usually whitish-gray, with the periphery deeply pigmented dark gray. The gland is invested by the digestive gland on all but the surface to which the hermaphrodite duct attaches. The surrounding digestive gland may be teased away rather easily from the hermaphrodite gland.

The *hermaphrodite duct* originates on the free surface of the hermaphrodite gland. The size and shape of this duct varies according to the age of the animal. In small, immature specimens, the duct is thin and often unconvoluted; as the animal increases in size, the duct becomes thicker and convoluted to a greater degree. The degree of pigmentation on the duct has been used in the diagnoses of some species of Succineidae by Pilsbry (1948). Degree of pigmentation is of no taxonomic value, because most series of all species considered in the present paper have shown extreme variation in this character. The hermaphrodite ducts of different individuals vary from deeply pigmented to light-colored and immaculate. It is worth noting that pigmentation of any internal organ is too variable to be of taxonomic importance. Furthermore, there is seemingly no correlation between age of the animal and degree of pigmentation of any structure.

The hermaphrodite duct terminates at the *fertilization sac*, situated at the base of the seminal vesicles. This sac sometimes is and sometimes is not the same color as the seminal vesicles.

The *seminal vesicles* of all individuals examined are paired; Pilsbry (*op. cit.*) reported this to be the prevalent condition among species of Succineidae. The two structures are occasionally equal in size, but generally unequal; in a series of any species in Kansas, the relative sizes of the seminal vesicles varies considerably.

The albumin gland is often the largest organ of the genitalia, especially in *Quickella*. The ventral proximal portion of the gland contains the fertilization sac and seminal vesicles. Albumin for the

ova is supposedly supplied by this gland, which in *Helisoma trivolvis* opens through a duct into the fertilization sac (Abdel-Malek 1954: 114). The albumin gland is usually pale, although it may be pigmented to varying degrees.

The term *oviduct* is here used in preference to uterus, because all members of the Family Succineidae are oviparous; the term "uterus" should be reserved for use in animals that are viviparous or ovoviviparous.

The size of the oviduct varies with the stage of sexual development of the animal. In immature animals the oviduct is smaller in diameter and more compact; its bulk may be exceeded by that of the prostate gland. In sexually mature animals the distended oviduct may obscure the penis, vagina, and seminal receptacle. This distention is especially obvious in large individuals of *Succinea concordialis*.

The term *seminal receptacle* is synonymous with "spermatheca"; both words seem equally applicable. Sperm introduced during mating are stored in this organ (Abdel-Malek, *op. cit.*). It is usually globular, although it may be elongate-oval in *Quickella vagans*. The size of the structure varies widely in some series of animals. The duct of the seminal receptacle originates on the oviduct at varying positions, according to the species. The duct is long and slender in *Succinea concordialis*, and short and thick in *S. ovalis*. Intermediate stages are found in other species. The portion of the female tract below the origin of the duct of the seminal receptacle is termed the vagina.

A nearly infallible rule seems to be that the seminal receptacle is associated with the left salivary gland, for in most individuals, the seminal receptacle or its duct is connected with this salivary gland by connective tissue. The seminal receptacle and intestine may be in actual contact, or they may be separated and joined by connective tissue.

The relative length of the *vagina* is constant within a species, but varies among species of the Family Succineidae. In *Succinea ovalis* and *Oxyloma retusa* the vagina is nearly as long as the penis; it is much shorter than the penis in *Quickella vagans*, *Q. wandae*, *Succinea concordialis*, *S. vaginacontorta*, and *S. pseudavara*. A peculiar torsion in the vagina is the primary distinguishing character of *S. vaginacontorta* (Lee 1951b).

The *prostate gland* is relatively large and conspicuous in *Quickella*, *Oxyloma*, and *Succinea ovalis*. In the remaining species of suc-

cineids occurring in Kansas, this gland is smaller. Contrary to the description by Pilsbry (1948:835), in which the prostate gland of *Succinea concordialis* is termed large, this gland is relatively small in this species in Kansas. In young *Quickella* and *Oxyloma*, the size of the prostate gland frequently exceeds that of the oviduct.

The term *vas deferens* is applied to the sperm duct from the point at which it leaves the prostate gland until it inserts on the distal end of the penis; its length and diameter are variable. It is long and relatively thin in *Oxyloma retusa* and *Succinea ovalis*, but shorter and thicker in *S. concordialis*. Intermediate conditions prevail in other species. Usually, the distal portion of the vas deferens is differentiated into an *epiphallus*, which in turn inserts on the penis. The epiphallus reaches its greatest differentiation in *Oxyloma* and is completely contained within the penial sheath in that genus. In *Succinea*, the epiphallus may or may not be completely contained within the sheath. An epiphallus is not distinctly differentiated in *Quickella*, although the vas deferens thickens as it enters the penis. In this study, a short epiphallus is considered to be present in *Quickella* beginning at, or near, the insertion of the penial retractor muscle on the sperm duct. The *penis* has been used extensively as a diagnostic feature in species of the Family Succineidae. In two genera, *Oxyloma* and *Succinea*, the penis is surrounded by a sheath, which varies in thickness and other characters among the various species. In *Quickella*, a penial sheath is not present.

The penis of *Oxyloma* possesses a structure termed an *appendix*, a small protuberance situated approximately at the point where the epiphallus inserts. The size, shape, and position of this appendix has been given considerable taxonomic weight in diagnosing species of *Oxyloma* (Pilsbry, 1948); several species have been diagnosed almost exclusively upon the appearance of the appendix. It has become evident to me, however, that the appendix varies within a population, from a small, blunt structure, scarcely evident, to one that is longer and tapering. It seems obvious that variations in the appendix are not specifically diagnostic. All populations of *Oxyloma* discovered in Kansas are considered to be *Oxyloma retusa*.

Quickella is unique among genera of Succineidae in Kansas in lacking a penial sheath. The penis possesses an appendix that is usually larger than the penis. Lee (1951a) believed that the terms penis and appendix are not applicable in *Quickella*, because he considered these structures to be elaborations of the vas deferens. However, in the present discussion, the standard interpretation of penis and appendix is retained.

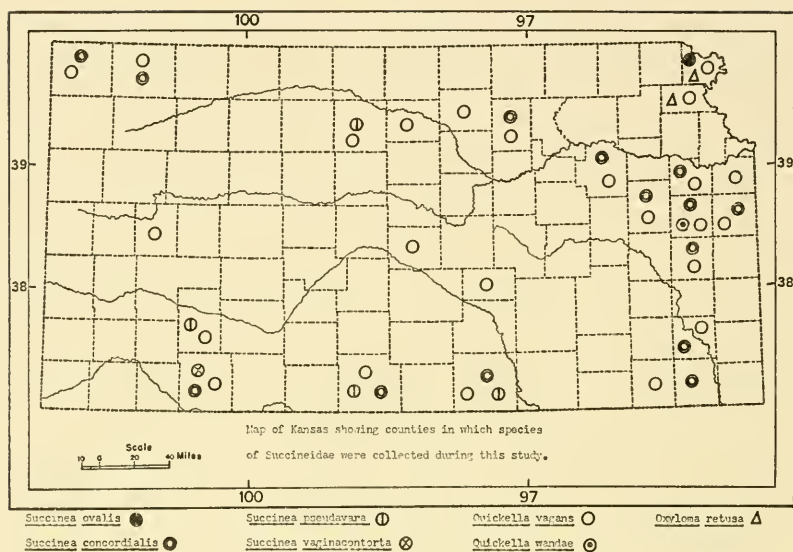


FIG. 1. Map of Kansas showing counties in which the seven species of Succineidae were collected in the course of this study. For each of four species, each symbol represents more than one record-station of occurrence; for example, although only one symbol for *Quickella vagans* is shown in Douglas County, collections of this species were made from several widely spaced localities within the county. For *Succinea pseudavara*, each symbol represents one collection. For *Succinea vaginacontorta* and for *Quickella wandae*, each symbol represents one specimen.

KEY TO THE SPECIES OF THE FAMILY SUCCINEIDAE IN KANSAS

1. A. Penial sheath not present; large appendix present which equals, or exceeds, length of penis. 2
- B. Penial sheath present. Appendix, if present, smaller than penis . . . 3
2. A. Appendix approximately equal to, or slightly longer, than penis, *Quickella vagans*
- B. Appendix much longer than penis due to presence of outgrowth from distal end; this outgrowth may be thrust "papilla-like" into appendix, *Quickella wandae*
3. A. Appendix present on distal end of penis *Oxyloma retusa*
- B. Appendix not present on penis 4
4. A. Vagina having prominent torsion just above entrance to genital atrium *Succinea vaginacontorta*
- B. Vagina lacking torsion 5
5. A. Vagina nearly as long as penis; duct of seminal receptacle surrounded by loop of oviduct *Succinea ovalis*
- B. Vagina much shorter than penis; duct of seminal receptacle not surrounded by loop of oviduct 6

6. A. Vas deferens flattened, wide, becoming incorporated with sheath of penis soon after crossing junction of penis and vagina; foot of animal possesses prominent dark gray flecks over entire surface

Succinea concordialis

B. Vas deferens not flattened, thin; becomes attached to sheath of penis distally; foot of animal with pigmentation concentrated primarily anteriorly and on posterior tip *Succinea pseudavara*

ACCOUNTS OF SPECIES

Succinea ovalis Say

(Plate I B, K, L; figures 2, 10a)

Succinea ovalis Say, 1817, Jour. Acad. Nat. Sci. Philadelphia, vol. 1, p. 15; DeKay, in part, 1844, Nat. Hist. New York, Mollusca, p. 53, pl. 4, fig. 52; Pilsbry, 1908, Proc. Acad. Nat. Sci. Philadelphia, p. 45, with var. *optima*, p. 46, and var. *chittenangoensis*, p. 49; Walker, 1928, Terrestrial Mollusca of Alabama, p. 167; Walker, 1904, Sixth Rep. Michigan Acad. Sci., p. 187; Ingram, 1943, Nautilus, vol. 56, p. 92; Pilsbry, 1948, Land Mollusca of North America, vol. 2, p. 801, figs. 429-432.

Helix (Cochlohydra) ovalis Say, Ferussac, 1822, Tabl. Syst. Limaçons, p. 26; Hist. Nat. Moll., pl. 11a, fig. 1.

Succinea ovatis Leidy, 1851, in Terr. Moll., vol. 1, pp. 213, 231, pl. 13, figs. I-III.

Succinea obliqua Say, 1824, in Appendix to Keating's Narrative Exped. source St. Peter's River, etc., Major Long's Second Expedition, vol. 2, p. 260, pl. 15, fig. 7; W. G. Binney, 1878, Terr. Moll., vol. 5, p. 423, and of most authors of the last century.

Succinea campestris Say, Gould, 1841, Invertebrates of Massachusetts, p. 195, fig. 126; DeKay, t. c., p. 53, pl. 4, fig. 54. Not *Succinea campestris* Say.

Succinea totteniana Lea, 1841, Trans. Amer. Philos. Soc., vol. 2, p. 32; W. G. Binney, 1878, Terr. Moll., vol. 5, p. 425, pl. 67b, fig. 2.

Helix (Cochlohydra) putris, Ferussac, Tableau Syst. fam. Limaçons, p. 26, no. 9; Hist. Nat. Moll., pl. 11a, fig. 9.

Succinea putris L., Cockerell, Nautilus, vol. 6, p. 30.

Type locality: Philadelphia, Pennsylvania.

Shell: "oval, inflated, thin, translucent, of a greenish-yellow tint, the summit paler or reddish; glossy; lightly marked with wrinkles of growth. Whorls two and a half, strongly convex, the last inflated, convex throughout. The aperture is ovate, about three-fourths the length of shell" (Pilsbry, 1948:802). The shells of Kansas specimens agree closely with this description, excepting the ratio of length of aperture to the length of shell, which averages somewhat less than three fourths (see below). The shell is usually the same color over its entire surface; the "reddish summit," present in the living state, is due to coloration of the brown digestive gland in the apex. Because of its distinct appearance at all stages of growth and its limited distribution in Kansas, the shell is seldom, if ever, mistaken for that of any other species of succineids in the State.

TABLE 1. Measurements of Shells of *Succinea ovalis* Say

length	diameter	length of aperture	diameter of aperture
18.8 mm.	10.8 mm.	12.0 mm.	8.6 mm.
11.6	6.9	8.8	6.0
17.4	9.4	11.7	7.4
15.2	8.6	10.4	6.8
9.8	5.7	7.1	4.5

From shells of 47 specimens, collected on 9 April, 1955, near Iowa Point, Doniphan County, the following average ratios were obtained:

$$\frac{\text{Diameter of shell}}{\text{Length of shell}} = 59\%, \text{ ranging from } 55\% \text{ to } 63\%$$

$$\frac{\text{Length of aperture}}{\text{Length of shell}} = 70\%, \text{ ranging from } 59\% \text{ to } 75\%$$

$$\frac{\text{Diameter of aperture}}{\text{Length of aperture}} = 68\%, \text{ ranging from } 62\% \text{ to } 76\%$$

Soft anatomy: The external appearance of the living animal varies considerably, as is true with most species of Succineidae in Kansas. The ground color of the foot is usually pale yellow; the sole is always yellow-orange, the periphery possessing darker orange color than the center. The sole is seemingly never pigmented.

Although some specimens are nearly immaculate, some pigmentation usually is present. Pigmentation varies from a faint gray stippling anteriorly on the sides of the head and foot, to dark gray vertical bars extending the entire length of the foot. In some examples, there is whitish stippling on the sides of the foot and under the collar, giving a glistening appearance to the animal when viewed under a dissecting microscope. The top of the head is invariably pigmented. The majority of specimens possess dark gray pigmentation evenly distributed over the dorsal surface of the head, in the area bordered laterally by the tentacular retractor muscles, which are visible through the epidermis of the snail.

The pattern of markings of the mantle over the lung varies markedly; the color in this species is ordinarily some shade of brown.

The jaw of *Succinea ovalis* is unique among Kansas succineids in possessing accessory ribs, in addition to the usual median projection (Fig. 10a).

Genitalia (Fig. 2): The genitalia of *Succinea ovalis* are distinctive among the species under consideration in several respects. The base of the duct of the seminal receptacle is as large in diameter, frequently larger, than the oviduct at its point of origin, but narrows

before reaching the globular seminal receptacle. The oviduct describes a loop around the duct of the seminal receptacle. This feature is diagnostic of *Succinea ovalis* in Kansas. The penis is large, completely filling the sheath. The vagina is nearly as long as the penis.

Genitalia are white except that the hermaphrodite duct, prostate gland, and seminal vesicles are invariably pigmented to some degree. The prostate gland is large and usually brown. The vas deferens is long and sinuous and differentiated into a distinctly thicker epiphallus beyond the point of insertion of the penial retractor muscle. The epiphallus is invariably free from the penial sheath, the epiphallus usually producing a sigmoid flexure. The penial retractor muscle is relatively thick and of equal diameter throughout its length.

The appearance of the free, looped epiphallus varies from specimen to specimen, but the loop is always present.

Distribution: *Succinea ovalis* barely enters northeastern Kansas in Doniphan County, inhabiting bluffs along the Missouri River. Numerous specimens have been collected from these bluffs along Kansas Highway 7, from Iowa Point to White Cloud (Doniphan County). Baker (1902:219) gives its distribution as eastern and central parts of northern United States, and west to Manitoba, Canada, and south to Arkansas and Georgia. This would place the western limit of its range in Kansas.

In Kansas, *Succinea ovalis* was generally found in shaded, damp situations along the base of bluffs, sometimes at considerable distance from the river. Invariably, the snails were on the ground under a protective cover of grass, leaves and twigs. A series of approximately fifty living specimens was collected on 9 April, 1955, from a low, wooded hill overlooking the Missouri River at White Cloud. On most other occasions, fewer specimens were found at any given time, generally six to twelve, but in April, 1956, seventeen specimens, ranging from immature to adult, were found in a small ravine filled to a depth of two feet with dead leaves. The snails, some of which were hibernating, were clinging to leaves.

General remarks: Strandine (1941:86) studied the ecology of a population of *Succinea ovalis* on a flood plain in Illinois. He found that the available leaf-mold seemingly influences population density, which "increases in the spring and early summer when the available leaf-mold is greatest." Strandine further found that "fluctuations in the density of the *Succinea ovalis* population coincides with the

fluctuations in the soil moisture, the organic matter, and the pH; the snail population increasing when the pH is increasing and the soil moisture and organic matter are decreasing."

Shimek (1935:6) found *Succinea ovalis* generally distributed throughout Iowa in wooded areas, especially in low alluvial bottomlands. He noted a population twenty-five to seventy-five feet above the river, entirely above the highest flood level.

Parasites: Ingram and Hewitt (1943:92) reported the occurrence of the sporocyst of a trematode (*Leucochloridium*) in *Succinea ovalis* in New York State. The sporocyst is banded with shades of brown, white, and green. Sporocysts, presumably of *Leucochloridium*, have been observed in Kansas in three individuals of *S. ovalis*, intertwined among the organs of the reproductive system.

Ellis (1926:140) reported that the sporocyst (*Leucochloridium*) is a stage in the life cycle of the fluke *Distomum*; the brightly colored branches in the tentacles of the snail (*Succinea putris*) attract the attention of birds, which peck off the tentacles and infect themselves. According to Ellis, the snail then grows a new tentacle!

Succinea concordialis Gould

(Place I F, I; figures 3, 10b)

Succinea concordialis Gould, 1848, Proc. Boston Soc. Nat. Hist., vol. 3, p. 38 (Lake Concordia); 1851, in Binney, Terr. Moll., vol. 2, p. 82, pl. 67a, fig. 2; W. G. Binney, 1878, Terr. Moll., vol. 5, p. 418; 1885, Manual American Land Shells, p. 441; Pilsbry and Ferriss, 1906, Proc. Acad. Nat. Sci. Phila., p. 159, figs. 11, 12; F. C. Baker, 1939, Fieldbook Illinois Land Snails, p. 123, figs.; Pilsbry, 1948, Land Mollusca North America, vol. 2, p. 833, figs. 452-454.

Succinea munita Binney, 1851, Terr. Moll., vol. 1, p. 128 (*nomen nudum*), teste W. G. Binney.

Succinea forsheyi Lea, 1864, Proc. Acad. Nat. Sci. Philadelphia, p. 109; Jour. Acad. Nat. Sci. Philadelphia, ser. (2), vol. 6, p. 178, pl. 24, fig. 107.

Succinea haleana Lea, 1864, Proc. Acad. Nat. Sci. Philadelphia, p. 109.

Succinea halei Lea, Jour. Acad. Nat. Sci. Philadelphia, ser. (2), vol. 6, p. 180, pl. 24, fig. 110.

Succinea witteri Shimek, 1913, Nat. Hist. Bull. State Univ. Iowa, vol. 6, p. 31, pl. 1, figs. I-IV.

Shell: "obliquely ovate, elongate, reflexed, apex acute, thin but firm, transparent, shining, feebly striated lengthwise and spirally, color pale honey yellow, with the tip ruddy; whorls three and somewhat more, very oblique . . .; aperture ample, not less than two-thirds the length of the shell, well-rounded at the base; . . . a broad, thin callus covers the left margin, which is slightly detached anteriorly, so as to form the rudiment of an umbilicus" (Pilsbry, 1948: 833).

TABLE 2. Measurements of Shells of *Succinea concordialis* Gould

length	diameter	length of aperture	diameter of aperture
11.8 mm.	6.5 mm.	8.0 mm.	4.8 mm.
13.4	7.8	9.7	6.0
13.7	7.3	9.6	5.5
12.7	7.2	9.0	5.3
11.0	6.0	8.0	4.6
9.1	4.9	6.1	3.6

In all series of *Succinea concordialis* examined from Kansas, the ratio of the length of shell to length of aperture approximates 70 per cent; this same ratio is present in *Succinea ovalis*. However, the shells of the two species differ in the average ratio of the diameter of aperture to length of aperture (60 per cent in *S. concordialis*, 70 per cent in *S. ovalis*).

TABLE 3. Average Ratios Derived from Dimensions of Shells of *Succinea concordialis*

Locality	No. shells	Date collected	$\frac{D}{L}$	$\frac{LA}{L}$	$\frac{DA}{LA}$
Lone Star Lake, Douglas Co.	13	16 Aug., 1955	.55	.70	.59
Sharon, Barber Co.	9	3 Apr., 1956	.57	.65	.61
Lawrence, Douglas Co.	8	16 May, 1956	.56	.70	.62
State Lake, Meade Co.	8	3 June, 1956	.56	.68	.62
Alma, Wabamsee Co.	12	12 June, 1956	.54	.70	.59

The shells of adult specimens of *Succinea concordialis* are not easily confused with other species in Kansas. The shining surface and ruddy apex is characteristic. However, shells of immature specimens are often without the ruddy apex and may be confused with those of *Quickella vagans*.

Type locality: Lake Concordia, Louisiana.

Soft anatomy: In the living state, the animal is easily identified by the characteristic black or dark gray, white-spotted, mantle, which is seen through the transparent shell. Pilsbry (1948:834) states that the spots are yellow in this species, but all specimens seen by me from Kansas possessed white spots, which appeared yellow when viewed through the shell. The foot is light gray, flecked with dark gray. This pigmentation is more or less evenly distributed over the exposed portion of the body when the animal is active. The dark maculations are larger than those on any other species of Succineidae in Kansas. Pigmentation on the posterior tip of the foot and dorsally on the head is arranged in a pattern of vertical bars; this pattern is not exhibited on the sides of the foot. The sole is gray, sometimes tinged with yellow. A few specimens possess faint stippling on the sole of the foot.

Jaw (Fig. 10b).

Genitalia (Fig. 3): The genitalia of *Succinea concordialis* vary

little in populations in the state. The species in Kansas differs from the description given by Pilsbry (1948:835) primarily in one respect: the prostate gland is always relatively small in comparison to the oviduct and other organs of the genitalia. Pilsbry (*loc. cit.*) states that the prostate gland of this species is comparatively large; his accompanying illustration confirms his statement. It should be noted, however, that Pilsbry's description is based on rather small specimens from one locality (Del Rio, Texas). More than one hundred specimens have been examined from widely scattered localities in Kansas; the shells of these specimens ranged from less than 6 mm. in length (immature) to more than 14 mm. (adults).

The duct of the seminal receptacle is unusually slender in *Succinea concordialis* and originates low on the oviduct at approximately the level where the vas deferens crosses the junction of penis and vagina. The seminal receptacle is globular. The vas deferens is diagnostically short, wide, and somewhat flattened, becoming attached to the sheath of the penis immediately after crossing the junction of penis and vagina. The penial sheath is small in relation to the size of the complete genitalia; this size relationship is especially noticeable in large snails. The sheath is thin, semi-transparent, enclosing a relatively thin penis. A distal opening in the sheath, allowing the epiphallus partially to emerge, has been seen in a few small specimens, but in the great majority of specimens, the sheath is entire. The penial retractor muscle inserts on the distal end of the sheath. Penis and sheath may be dark gray, although they are usually immaculate.

The hermaphrodite duct is usually some shade of gray, never brown as in some other species of Succineidae in Kansas. The duct becomes tightly convoluted soon after leaving the hermaphrodite gland, then straightens before inserting at the fertilization sac. Approximately two-thirds of the duct is convoluted.

Distribution: *Succinea concordialis* seemingly occurs throughout Kansas (Map, Fig. 1); in numbers it is exceeded only by *Quickella vagans*. Pilsbry (1948:834) cites the following states in which this species has been reported: Texas, Louisiana, Arkansas, Missouri, Illinois, Iowa, Tennessee, Alabama, and Florida. Webb (1954:10) reported this species from Marshall County, Oklahoma. Franzen and Leonard (1942:339) noted its occurrence in Kingman County, Kansas.

Succinea concordialis has been found in Kansas in two distinct habitats. Generally, it occurs near the edges of streams in wet

situations, clinging to vegetation near or in water, or living in the wet leaf mold at the edge of the water.

Elsewhere, the species inhabits comparatively dry environments. In Meade County State Park, a number were found near the lake, in a low area overgrown by thick vegetation, but several isolated places were sandy and barren. The sand was only slightly damp. *S. concordialis* was found here, inhabiting the damper places in the sand. *Quickella vagans* was also present in approximately equal numbers. The only shade was provided by a dead bush.

On a few other occasions, *Succinea concordialis* was found in drier situations, and the species is observed in the open, exposed to the sun, more than other species of Succineidae in Kansas.

General Remarks: *Succinea concordialis* was reluctantly placed in the section *Calcisuccinea* by Pilsbry (1948:826) because the genitalia resemble superficially those of *S. campestris* Say, *S. luteola* Gould, and *S. l. floridana* Pilsbry. Webb (1954:10) has recently removed *S. concordialis* from *Calcisuccinea* and placed it in a new section, *Desmosuccinea*, characterized by the fusion of the pore in the distal end of penial sheath, which prevents the epiphallus from emerging in a loop as it does in species of *Calcisuccinea*. I have observed several immature specimens of *S. concordialis* that possessed a pore which allowed the epiphallus to emerge in a slight loop. Nevertheless, Webb's action of placing *S. concordialis* in a new section seems justified, because the pore in the penial sheath is seemingly always obliterated in the adult animal.

Parasites: One specimen of *S. concordialis* from Lone Star Lake, Douglas County, was infested by a fly larva, seemingly identical with those in several specimens of *Quickella vagans*.

Succinea vaginacontorta Lee

(Plate I C; figure 4)

Succinea vaginacontorta Lee, 1951, Occas. Pap. Mus. Zool.; Univ. Michigan, no. 533, p. 1, pls. 2, figs. 7.

"Shell is dextral, fully developed. Whorls 3, with suture only moderately impressed. Whorls which increase proportionately from the apex to the body whorl with no marked discontinuity in size. In life shell is a dull, translucent, light, horn yellow with greenish tones. Striae present and well raised. Epidermis of upper whorl eroded away revealing dull white deeper layers of shell, parietal wall with well developed callus, covering base of slightly curved columella. Aperture obliquely ovate with a slight flare at base of

outer lip. Interior of aperture with a thin shiny transparent sheen" (Lee, 1951b:2, description of holotype).

Shell of holotype: Length, 9.8 mm; width, 5.9 mm; aperture length, 5.7 mm; aperture width, 4.2 mm.

Type locality: Southwest corner of Sec. 18, T. 33S, R. 28W, approximately 8 miles south and 4 miles west of Meade, Meade County, Kansas.

I found only one specimen of this species; it was at Meade County State Park, 3 June, 1956, on a bank of an impoundment pond near the lake. The specimen was associated with numerous individuals of *Quickella vagans*. The animal remained unrecognized until dissected. Measurements of its shell are: length, 8.4 mm; diameter, 4.9 mm; length of aperture, 5.2 mm; diameter of aperture, 3.6 mm.

This shell generally fits the original description; the callus is not well developed, but the striae are quite pronounced.

Externally, "the animal is a dull, grayish white with the anterior part finely peppered with black pigment . . . the surface of this hermaphroditic animal is sufficiently transparent in the region of the genital furrow to expose the outlines of both the vagina and penis . . . the edge of the mantle may have a few to many concentrations of black pigment. Some appear gray. The rest of the mantle is finely reticulated" (Lee, 1951b:3).

Genitalia (Fig. 4): *Succinea vaginacontorta* is distinguished from all other known species of the Succineidae by the presence of a prominent torsion in the vagina, occurring slightly posterior to the junction of the vagina with the common genital atrium.

In the single specimen examined, the hermaphrodite duct is light gray. The unequal seminal vesicles are somewhat darker. The albumin gland, oviduct, prostate gland, and vagina are white. The penial sheath is relatively larger than in any other succineid examined and the epiphallus emerges from the penial sheath in a flattened loop. Distally, the penial sheath and vas deferens are peppered with gray. The prostate gland is small, and the vas deferens thick. The latter structure approaches the junction of penis and vagina and then rises to run parallel to the penial sheath until the vas deferens enters the sheath distally. The penial retractor muscle is thin and inserts on the penial sheath at the base of the free loop of the epiphallus. The seminal receptacle is small and globular, the duct originating immediately above the twisted portion of the vagina. The duct is long and slender.

The penial sheath is thick and resistant to cutting, more so than in any other species of the family known to occur in Kansas. As

Lee (1951b:5) indicated in his original description, the penis is enclosed in a sheath "of tough, fibrous, fuzzy, connective tissue". In other species of *Succinea* examined, the sheath is thin and usually semi-transparent. The penis is relatively thin in *S. vaginacontorta*.

General remarks: On the basis of the genitalia, Lee considered that the affinities of *Succinea vaginacontorta* were with the section *Calcisuccinea* Pilsbry, which includes *S. campestris* Say, *S. luteola* Gould, and *S. l. floridana* Pilsbry.

Webb (1953:216) has placed *S. vaginacontorta* in a separate section, *Heysuccinea*. He considered the distinctive torsion in the vagina, and the vas deferens being free from the junction of penis and vagina, sufficient justification to warrant this.

Distribution: *Succinea vaginacontorta* has been reported to occur only in Kansas. Webb (*op. cit.*) found the species at the following localities: Lawrence, Douglas County; south of Kingman, Kingman County; 6 miles north of Meade, Meade County; 3-4 miles north of Herington, Dickinson County.

Succinea pseudavara Webb

(Plate 1 D; figure 5)

Succinea pseudavara Webb, 1954, *Gastropodia*, vol. 1, no. 2, p. 10, figs. 8.

Shell: Amber-colored, rather polished, frequently coated with mud as in *Quickella vagans*; these two species may easily be confused. Transverse striae are less regular and riblike than in *Q. vagans*. The spire is approximately as long as the aperture. The apex is pink-brown, darker than the remaining whorls. The shell lacks the filelike papillae of *Q. vagans* and the revolving striae of *S. concordialis*.

Identification of *S. pseudavara* probably cannot be made from the shell alone, as Webb pointed out in his original description. He did not include measurements of shells. Several shells of this species from the bank of the Arkansas River in the City Park at Cimarron, Gray County, Kansas, measured as follows:

TABLE 4. Measurements of Shells of *Succinea pseudavara* Webb

length	diameter	length of aperture	diameter of aperture
7.2 mm.	4.3 mm.	5.0 mm.	2.9 mm.
8.1	4.7	5.4	3.3
8.2	4.9	5.5	3.2
7.0	4.0	4.5	2.6

TABLE 5. Average Ratios Derived from Dimensions of Shells of *Succinea pseudavara*

Locality	No. shells	Date collected	D	LA	DA
			L	L	LA
Cimarron, Gray Co.	8	3 June, 1956	.59	.66	.59
Medicine Lodge, Barber Co.	7	4 June, 1956	.53	.62	.57

Because specimens of *S. pseudavara* were found at only four localities, two of which yielded four snails, no generalities can be made from ratios derived from measurements.

Type locality: "About 1½ miles east of the University of Oklahoma Biological Station, at Lake Texoma, near Willis, Marshall County, Oklahoma" (Webb, 1954:18).

External appearance of animal: The color of the foot is grayish-white and lacks the brownish tint usually present in *Quickella vagans*, with which it may be confused. A small amount of gray stippling is present anteriorly on sides of foot and on top of head. The posterior tip of the animal also is obviously pigmented, in a vague pattern of vertical bars. The sole of the foot was pigmented in only two individuals. The pigmentation on the head and foot is much finer than the flecks present on *Succinea concordialis*, and is concentrated on the anterior and posterior parts of the animal. In *S. concordialis*, the pigmentation tends to be evenly distributed.

The pattern of the mantle resembles that of *Quickella vagans*. The ground color is usually translucent gray with darker gray present in the form of a reticulum. This darker gray is sometimes arranged in peripheral blotches, simulating the usual condition found in *Quickella*. A brownish tint on the mantle has been observed in a few specimens. The rim of the mantle is white. The kidney usually is not obvious when viewed through the shell.

The eye-stalks are lightly pigmented and there is a narrow stripe of dark gray extending medially between their bases. The dorsal portion of the head and foot, when extended, is evenly pigmented gray on the surface bordered by the dark colored tentacular retractor muscles.

Genitalia (Fig. 5): *Succinea pseudavara* is obviously related to *Succinea concordialis* in details of its genitalia. The penial sheath of the former is large and ovate, enclosing a penis similar in appearance to that of *S. concordialis*. The penis is relatively thick distally, tapers as it approaches the genital atrium and increases abruptly in diameter before reaching the atrium. Most specimens of *S. pseudavara* examined by me agreed with Webb's description (1954:18) in lacking a pore on the distal end of penial sheath, a loop of the epiphallus, therefore, not appearing. In two specimens, however, a pore was present and the epiphallus emerged in a loop. Approximately thirty specimens were dissected.

The seminal receptacle is globular; its duct is long and slender. The duct originates low on the oviduct; the vagina is therefore short. The prostate gland is similar in appearance to that of *S.*

concordialis, but is relatively larger. The vas deferens is somewhat thinner than in *S. concordialis* and is not flattened, which is one of the best methods of distinguishing the genitalia of the two species. The vas deferens reaches the junction of penis and vagina, then rises to extend along the penial sheath before becoming incorporated distally in the sheath and penial retractor muscle. The penial retractor muscle is thin. The seminal vesicles are usually darker than the hermaphrodite duct and were relatively small in the specimens examined.

The entire reproductive system is colored varying shades of gray; the brownish color frequently seen in species of *Quickella* has not been observed in *S. pseudavara*.

Distribution: This species previously has been reported only from Oklahoma (Webb:1954). In the course of my study, specimens were collected from four counties in Kansas: Osborne, Gray, Barber, and Sumner.

Succinea pseudavara was found along the edges of streams in Kansas, associated with *Quickella vagans* and *S. concordialis*. The shade provided by bridges seems to attract this species, although specimens were also collected in more exposed places, under the concealment afforded by grass and other vegetation. The shell may be coated with mud.

General remarks: I agree with Webb (*op. cit.*) that *S. pseudavara* is related to *S. concordialis*. The genitalia of the two species are similar in several significant respects: (1) the penes of both species are morphologically similar; (2) the duct of the seminal receptacle originates at approximately the same position on the oviduct in both species; (3) the epiphallus does not ordinarily appear in a free loop from the sheath of the penis; (4) the size and insertion of the penial retractor muscle are alike in both species; and (5) the vas deferens reaches the base of the junction of the penis and vagina in both species.

Webb placed *S. pseudavara* and *S. concordialis* in a new section, *Desmosuccinea*. The striking similarities in the genitalia of the two species certainly warrants this action.

Oxyloma retusa (Lea)

(Plate I G, H; figures 6, 7)

Succinea retusa Lea, 1834, Trans. Amer. Philos. Soc., vol. 5, p. 117, pl. 19, fig. 86; (Ohio, near Cincinnati).

Succinea higginsii "Bland, Nov. spec.", Tryon, July, 1866, Amer. Jour. Conch., vol. 2, p. 237, pl. 17 (2), fig. 24; Bland, October, 1866, same volume, p. 373, pl. 17, fig. 24; W. G. Binney, 1885, Manual American Land Shells, p. 198, fig. 206.

Succinea retusa magister Pilsbry, 1899, *Nautilus*, vol. 12, p. 103; 19:109, fig. 2; Walker, 1906, *Mollusca of Michigan*, p. 502, fig. 110; F. C. Baker, 1939, *Fieldbook Illinois Land Snails*, p. 125, fig. B.
Succinea calumetensis Calkins, 1878, *Valley Naturalist*, vol. 1, no. 11, p. 57, text fig.; cf. Walker, 1906, *Mollusca of Michigan*, p. 502, fig. 108.
Oxyloma retusa (Lea), Pilsbry, 1948, *Land Mollusca of North America*, vol. 2, p. 785, figs. 421, 422C.

Shell: "ovately oblong, very thin, pellucid; spire short; whorls 3; aperture below dilate and drawn back. Diam. 0.3, length 0.7 of an inch. . . . It differs so much from any of the described species in the dilation and retraction of the inferior part of the aperture that I have not hesitated to consider it new" (Lea's description, quoted by Pilsbry, 1948:786).

The shell of this species is an intense yellow-horn color. Whorls vary from 2 to 3, depending on the age of the animal. The suture between body whorl and apex is not prominent. The whorls are less convex than in any other known species of the Succineidae in Kansas. The aperture is elongate, occupying 70 percent of the total length of the shell. In some populations, individual shells vary in greatest diameter to a marked extent. Lee (1951a) has pointed out that the parietal area and outer margin of the peristome tends to be straight, producing in outline an aperture resembling an elongate teardrop.

Type locality: Ohio, near Cincinnati.

TABLE 6. Measurements of Shells of *Oxyloma retusa* (Lea)

length	diameter	length of aperture	diameter of aperture
12.6 mm.	6.8 mm.	9.2 mm.	5.6 mm.
11.7	6.5	8.5	5.4
10.3	5.9	7.3	4.7
14.1	7.0	10.1	6.2
9.0	5.0	6.8	4.2

TABLE 7. Average Ratios Derived from Dimensions of Shells of *Oxyloma retusa*

Locality	No. shells	Date collected	$\frac{D}{L}$	$\frac{LA}{L}$	$\frac{DA}{LA}$
Muscotah, Atchison Co.	16	5 Apr., 1955	.55	.73	.64
Iowa Point, Doniphan Co.	10	4 Sept., 1955	.47	.68	.60
Iowa Point, Doniphan Co.	12	21 Apr., 1956	.54	.70	.60

The diameter of the shell is approximately 50 percent of the length of shell in *Oxyloma retusa*. A few series were collected in which the diameter of shells averaged less than 50 percent of the length.

External appearance: Baker (1939:125) reported that *Oxyloma retusa* appears in two color phases: dark in spring, and light in summer and autumn. Both color phases occur in Kansas. In the light phase, the foot of the animal is light gray, or yellow, with

clumps of fine stippling present laterally and dorsally on the head and foot. Pigmentation is more profuse anteriorly, in some specimens disappearing toward the posterior half of foot. The sole of the foot may be pigmented. In the darker color phase, considerably more pigment is present on the head, mantle, and foot. The lateral and anterior pigmentation on the foot of a few specimens may be arranged in vertical rows similar to the pattern exhibited in *Quickella*. The underside of the rim of the mantle is usually pigmented, the pigment being concentrated in the vicinity of the opening to the lung.

The mantle over the lung is stippled with fine dark gray dots, present on a gray or tan background. The stippling is uniformly distributed anteriorly on the mantle, but becomes dispersed posteriorly, often appearing in isolated groups on the posterior portion of the animal. Sparse stippling is often present on the rim of the mantle. As in *Quickella*, the pigmentation on the mantle may be concentrated peripherally into blotches, from which faint streaks radiate toward the kidney.

Genitalia (Figs. 6, 7): *Oxyloma retusa* is characterized by the presence of a small appendix on the penis, at about the position where the epiphallus inserts (Fig. 7). The appendix is extremely variable in size and shape within the species; this variability also occurs within a population. In large series of animals the appendix may vary from a blunt, scarcely developed protuberance, to a slender, tapering structure. The size of the appendix seemingly is not correlated with the size of the animal. The epiphallus is completely contained within the penial sheath and may be coiled or relatively straight. The penis is large and may be straight within the sheath, but frequently is bent or coiled in a half turn. When the sheath is opened, the position of the appendix depends upon the degree of coiling of penis and epiphallus (Fig. 7).

The seminal receptacle is globular; its duct is short and of approximately the same diameter throughout its length. The duct originates high on the oviduct, resulting in a vagina the length of which is equal to that of the penis. The prostate gland is large and usually speckled with gray. The vas deferens is long, reaching to the junction of penis and vagina, and then rising to insert on the distal end of the epiphallus after entering the penial sheath. The albumin gland is relatively small in comparison with oviduct and prostate gland. As in all species of Succineidae in Kansas, the degree of pigmentation of the genitalia varies from animal to animal.

Distribution: *Oxyloma retusa* was collected only in Atchison and Doniphan counties in northeast Kansas. In Atchison County, a large population exists in a marsh maintained by artesian flow, 1½ miles south of Muscotah. Although the snails were abundant there in 1955, the population has since declined.

In Doniphan County, specimens were taken in considerable numbers throughout the course of this investigation. A favorable habitat for *Oxyloma retusa* is roadside ditches along Kansas Highway 7, in the vicinity of Iowa Point. *Succinea ovalis* inhabits the bluffs above these ditches. *O. retusa* may be seen on vegetation several feet from the ground. Specimens were taken also from dead vegetation on the ground and from the wet banks near water.

Elsewhere in North America, *O. retusa* has been reported from Ohio, Illinois, Iowa, Minnesota, North Dakota, and Montana (Pilsbry 1948:786).

General remarks: Alice E. Leonard (1943:240) reported *Succinea haydeni* Binney (= *Oxyloma haydeni*) at Meade County State Park and noted that "this snail thrives on the moist marshes and borders of the pools in the artesian basin, where it is frequently found on watercress." A series of shells in the University of Kansas Museum of Natural History, collected by her from Meade County, are large, ranging from 15 mm. to 17 mm. in length. The shells generally agree in characters with those determined to be *Oxyloma retusa* from Atchison and Doniphan counties. The average ratios of the shells from Meade County are given below, along with average ratios obtained from a series of *O. retusa* from Doniphan and Atchison counties.

TABLE 8. Table of Average Ratios of *Oxyloma*

Locality	No. shells	Species	$\frac{D}{L}$	$\frac{LA}{L}$	$\frac{DA}{LA}$
Meade County State Park. . . .	7	<i>Oxyloma haydeni</i> ?	.49	.72	.59
Muscotah, Atchison Co.	16	<i>Oxyloma retusa</i>	.55	.73	.64
Iowa Point, Doniphan Co.	10	<i>Oxyloma retusa</i>	.50	.70	.59

In June, 1956, I visited Meade County State Park and searched in vain for specimens of *Oxyloma*. A resident of Meade County informed me that several years ago, probably in 1953, considerable grading was done in the artesian marshes by the use of bulldozers. Perhaps the population of this species was destroyed in the process; at any rate, neither shells nor live snails were discovered in June of 1956. Because of the appearance of the shells mentioned above, however, I believe that the species of *Oxyloma* from Meade County

is *O. retusa*, although final judgment concerning the identification should be reserved until the animal is found and examined anatomically.

Quickella vagans (Pilsbry)

(Plate I E, J; figure 8)

Succinea campestris vagans Pilsbry, 1900, *Nautilus*, vol. 14, p. 74.

Quickella vagans (Pilsbry), 1948, *Land Mollusca of North America*, vol. 2, p. 843, fig. 456.

Shell: "Globosely oval shape, very convex whorls and rather dull or weakly glossy surface, which is irregularly and often in places somewhat coarsely wrinkled. It is small, fragile, with only $2\frac{1}{2}$ to $2\frac{3}{4}$ whorls in the type lot, in southern specimens as many as three whorls; subtranslucent ecru-olive, without the opaque whitish streaks or the whitish inner layer of *campestris*" (Pilsbry, 1948:843).

The shell of this species varies strikingly within Kansas. The number of whorls ranges from $2\frac{1}{2}$, in small individuals, to nearly 4. The color varies from light yellow to reddish brown. In some populations, the whorls tend to become flattened, giving the shell an elongate appearance. Striae are not well developed, although mature shells are never so glossy as those of *Succinea concordialis*. The shells of living snails are frequently coated with mud and debris.

The shells of young specimens may be confused with those of young *S. concordialis*.

TABLE 9. Measurements of Shells of *Quickella vagans* (Pilsbry)

length	diameter	length of aperture	diameter of aperture
12.6 mm.	6.3 mm.	7.3 mm.	4.6 mm.
11.5	6.2	7.1	4.7
10.0	5.8	6.6	4.4
9.0	5.0	5.4	3.3
6.7	4.2	4.3	3.0

TABLE 10. Average Ratios Derived from Dimensions of Shells of *Quickella vagans*

Locality	No. shells	Date collected	$\frac{D}{L}$	$\frac{LA}{L}$	$\frac{DA}{LA}$
Lone Star Lake, Douglas Co.	16	28 July, 1955	.56	.61	.66
Lawrence, Douglas Co.	30	4 Aug., 1955	.55	.64	.63
Sterling, Rice Co.	6	1 Apr., 1956	.61	.62	.70
Sharon, Barber Co.	6	3 Apr., 1956	.57	.60	.67
State Park, Miami Co.	10	12 May, 1956	.57	.57	.71
Burlingame, Osage Co.	10	12 June, 1956	.53	.61	.65

Type locality: Cape May Point, New Jersey.

External appearance of animal: *Quickella vagans* exists in 2 color phases, light and dark. In the dark phase, there is a characteristic

pattern of vertical bars completely around the foot. These bars always are interrupted ventrally, then continue a short distance to the sole. Anteriorly, four or five bars of pigment are present on the head, extending from the base of the eyestalks ventrally to near the mouth. These anterior bars tend to slant medially as they approach the mouth.

In the light phase, the pigmentation is scanty, or absent. If traces of the vertical bars persist, they invariably are on the anterior part of the animal.

The ground color is variable. It may be cream white or gray, or brownish-orange. There is nearly always a tinge of brown present on the animal, either laterally on the foot and/or dorsally on the head. The color of the sole of the foot is similar to the remainder of the foot, usually with varying degrees of brown. In some specimens the sole is stippled, but ordinarily it is immaculate.

There is seemingly no correlation between size of the animal and the color phase; both phases and intermediates usually are represented within a population.

The mantle of *Quickella vagans* also varies considerably although some modification of a basic pattern is present in most specimens. This pattern consists of streaks of pigmentation radiating inward toward the kidney from the margin of the mantle. Peripherally, the pigmentation is concentrated in blotches, from which the radiating streaks originate. The color varies from gray to brown, and in some specimens may be so intense as to obscure the pattern. The kidney usually is bright yellow or orange, easily visible through the mantle, but this organ may be nearly invisible because of intense pigmentation on the mantle. The ground color of mantle over the lung is usually translucent gray, but may be brown. The color of mantle and foot are independent of one another; a specimen with a lightly pigmented foot may possess a dark mantle.

Genitalia (Fig. 8): The distinguishing characteristic of *Q. vagans* is the penis-appendix complex. The two structures are variable in their relative sizes, because the appendix is capable of infolding. The size of the appendix may be approximately equal to that of the penis, but is usually somewhat larger. There is no sheath investing the penis. Longitudinal ridges occur within the penis and appendix. From the distal end of the penis the epiphallus rises slightly for insertion of the penial retractor muscle, then descends, as the vas deferens, along the posterior surface of penis-appendix to the junction of penis and vagina. The penial retractor muscle inserts on the

epiphallus and sends a primary branch to the appendix; the penis proper is free of the retractor muscle, except for minor connectives.

The duct of the seminal receptacle originates low on the oviduct, somewhat as in *Succinea concordialis* and *S. pseudavara*. The length of this duct varies and is relatively much thicker than in the two species mentioned above. The seminal receptacle is sometimes globular, but is often elongate-oval. The vagina is short.

Distribution: *Quickella vagans* is generally distributed over the State and is by far the most abundant representative of the Succineidae in Kansas. Pilsbry (1948:844) records this species from New Jersey and North Carolina. Kagan (1949:38) was the first to discover that the genus *Quickella* occurs as far west as Michigan. Lee (1951a) later identified the species in Michigan. Webb (1953) reported it in Kansas. This species is undoubtedly distributed over much of North America, but has been, and is, confused with species of *Succinea*.

Q. vagans inhabits a variety of habitats. The majority of specimens collected by me were found near margins of streams and lakes. In such places, individuals generally occur on the ground under a protective cover of grass, leaves, and twigs, but some were above the ground attached to blades of grass and vegetation. An examination of the undersides of smooth logs and sticks lying on banks of streams often reveal specimens.

This species inhabits also dryer localities, sometimes at considerable distances from standing water. Specimens have been collected on the banks of dry streams in shady, deciduous woods. In June, 1956, large individuals were numerous in low, sandy, areas, barren of vegetation, in Meade County State Park of western Kansas. The sand was damp beneath small dead branches, scattered over the sand. Several large specimens of *Succinea concordialis* were associating with the *Quickellas*.

At Atwood Lake in Rawlins County, of northwestern Kansas, several examples of *Q. vagans* and *S. concordialis* were found in the dry bed of a stream draining into the lake. The snails were under logs and boards on the bed of the stream, shaded by trees. There was no standing water in sight; Atwood Lake was completely dry at the time.

In Johnson County, of eastern Kansas, a large population lived in a heavily wooded area, along the base of a small hill, under grass and brush, approximately $\frac{1}{4}$ mile north of De Soto. This locality is more than one hundred yards from the Kansas River.

Q. vagans invariably lives beneath logs or other vegetation and

has not been observed moving in places exposed to the rays of the sun; whereas, *S. concordialis* often is active in hot, dry places exposed to direct rays of the sun.

General remarks: As mentioned earlier, *S. avara* and *S. grosvenori* previously have been considered to be abundant in Kansas. However, collections studied by me from many localities in Kansas have failed to reveal either species, as well as other species of *Succinea* previously reported in this state. It seems that the variable shell of *Quickella vagans*, and perhaps that of *Q. wandae*, have been confused with species of *Succinea*. Additional collecting in Kansas may, of course, reveal the presence of additional species of *Succinea*, but I surmise that most shells previously regarded as *S. avara* and *S. grosvenori* were, in fact, *Quickella*. This statement is qualified because the distribution and abundance of *Succinea vaginacontorta* and *S. pseudavara* are imperfectly known; both species resemble *Quickella* and associate with it.

Parasites: Two kinds of parasites have been found to infest *Q. vagans* in Kansas. The least abundant of these parasites is a fly larva observed in five snails, four of which were collected at Lone Star Lake in Douglas County. Another infected snail was found near Coffeyville, Montgomery County. The larva lies partially against the reproductive system. The genitalia of some infected snails were relatively underdeveloped, when compared with uninfected snails of approximately the same size and from the same population. The external appearance of the snail is not altered by the presence of the parasite.

Dr. H. B. Hungerford of the Department of Entomology, University of Kansas, examined a larva and reported the larva probably to be a first instar of a muscoidean fly, species undetermined.

Dr. Clifford Berg, associated with the Cornell University Agricultural Experiment Station, and a specialist on fly larvae parasitic in snails, has reported the occurrence of fly larvae (*Dyctya expansa*) in *Oxyloma decampi gouldi* in Alaska (1953:631).

The second parasite found to infest *Q. vagans* is a small nematode. There are invariably many individuals of this parasite in an infected snail; the incidence of infection in *Q. vagans* is high. In one population from Miami County State Park, more than 50 percent of the snails were infected.

In Michigan, Kagan (1949:38) discovered that *Quickella* was infested by sporocysts of the trematode, *Leucochloridium*, but in my studies of several hundred *Q. vagans* from Kansas, no *Leucochloridium* was found.

Quickella wandae Webb

(Plate I A; figure 9)

Quickella wandae Webb, 1953, Jour. Tennessee Acad. Sci., vol. 28, p. 216, pls. 3, 4.

Shell: "very similar to that of *Quickella vagans* (Pilsbry), greenish yellow, epidermis brownish where thick, apex less obtuse than in *Quickella vagans*, size less. Umbilicus closed on the lower half of the columella, rarely partly unsealed" (Webb, 1953:216).

I found only one specimen of *Q. wandae*. It was obtained along with several specimens of *Q. vagans* on 8 April, 1956, from the bank of a small stream in Franklin County, Kansas.

The one shell examined by me possesses 2½ whorls. The color is greenish yellow. Striae are well developed on the body whorl, but are scarcely evident on the apex. A parietal callus is present, but is not prominent.

Webb did not include measurements of shells with his original description of this species. The one shell examined by me measured: length, 5.4 mm; diameter, 3.5 mm; length of aperture, 3.4 mm; diameter of aperture, 2.4 mm.

Type locality: 8½ miles south and ½ mile east of Alma, Wabaunsee County, Kansas.

External appearance of animal: Webb's original description, which referred to a drowned specimen, is as follows: "Rim of the mantle at aperture and exertile body flecked with brown; liver very light brown; grooves of the foot whitish; regions between the grooves blackish, fading posteriorly on the foot. Body anterior to the visceral pillar grayish, marked dorso-laterally on each side by an unpigmented line. Sole whitish, densely orange-flecked. Mantle of the lung whitish with about nine interrupted streaks of dash-like markings" (Webb, 1953:216).

In the one specimen examined by me, the lateral vertical bars are well developed around the entire foot. They are interrupted ventrally, as in *Quickella vagans*. The mantle pattern differs from the typical pattern of *Q. vagans*; instead, the dashlike markings mentioned in the description by Webb are present. The ground color of the mantle over the lung is light translucent gray.

Genitalia (Fig. 9): The diagnostic feature which serves to distinguish the two known species of *Quickella* in Kansas, is a peculiar white, smooth, extension on the appendix in *Q. wandae*, which lengthens this organ considerably more than the penis. Webb (*loc. cit.*) referred to this extension as a "glandular outgrowth" on the appendix.

The relationship of penial retractor muscle to the penis-appendix complex may offer an additional diagnostic character. In *Q. vagans*, the muscle inserts on the epiphallus, sending a primary branch to the appendix; the penis is nearly free of any contact with the muscle. In the one specimen of *Q. wandae* examined, the muscle inserts on the epiphallus and the primary branch attaches to the penis near the junction of penis and appendix; the appendix is free of the muscle. Whether or not this character is specific for *Q. wandae* is unknown, because of the lack of material.

The remainder of the genitalia of the one animal observed does not differ significantly from the same organs in *Quickella vagans*. The hermaphrodite duct is gold-colored, not pigmented. The seminal vesicles are of unequal size and lightly flecked with brown. The seminal receptacle and duct appear as they do in *Q. vagans*.

Distribution: *Q. wandae* has been reported only from Kansas. Webb collected specimens in four counties: Douglas, Leavenworth, Wabaunsee, and Anderson. The one specimen collected by me adds Franklin County to the known range. All specimens collected by Webb were found in rather shady, deciduous woods on well-drained, damp terraces.

General remarks: It seems that the shells of *Q. wandae* and *Q. vagans* are indistinguishable.

Webb (1953:216) states that the outgrowth or extension of the appendix of *Q. wandae* may be thrust "papilla-like" into the lumen of the appendix.

ORIGIN OF SPECIES OF SUCCINEIDAE IN KANSAS

The distribution of most of the Recent species of Succineidae known to live in Kansas now is too imperfectly known to ascertain their probable origin. *Succinea concordialis* has been reported from Texas, Louisiana, Arkansas, Missouri, Illinois, Kansas, Iowa, Tennessee, Oklahoma, Alabama, and Florida, but the species may range farther west than is presently known; I collected numerous specimens only 12 miles or so east of the Colorado line (banks of the Republican River, St. Francis, Cheyenne County, Kansas).

Oxyloma retusa, which has been reported to inhabit the north-central and northeastern United States (Ohio, Illinois, Minnesota, North Dakota, and Kansas), is in a genus the taxonomic status of which is in a confused state. In Kansas, the shells of *O. retusa* vary between different populations and probably this is true elsewhere. The distribution of this species probably is incompletely known.

Quickella vagans has been recorded from New Jersey, North Carolina, Michigan, and Kansas. Probably it occurs more widely and farther west than the mentioned occurrences indicate; several alleged species of *Succinea* from the western United States may belong to the genus *Quickella*.

S. vaginacontorta and *Q. wandae* are known only from Kansas, but probably occur elsewhere. *S. pseudavara* is known only from Kansas and Oklahoma; it also probably is more widely distributed than is known at present.

S. ovalis is the only species of the Succineidae for which the distribution in North America is well known. This species ranges throughout the northeastern two-thirds of that continent, and enters Kansas only in the extreme northeast part of Doniphan County, which is the northeasternmost county and at about the western limit of the range of the species. *Succinea ovalis* has entered Kansas probably from a northern or eastern route of dispersal.

SUMMARY

1. The Family Succineidae is represented in Kansas by three genera and seven known species. Shells of most species lack distinguishing characters and cannot be relied upon for purposes of identification.

2. The genitalia of these seven species are distinctive and furnish the most reliable means of distinguishing one species from another.

3. The four species of *Succinea* have in common a penis that lacks an appendix and that is contained within a sheath. *Succinea ovalis* is easily diagnosed because the duct of the seminal receptacle is surrounded by a loop of the oviduct. *S. vaginacontorta* possesses a large, thick penial sheath and is unique in that the vagina is twisted to a striking degree. The genitalia of *S. concordialis* and *S. pseudavara* are similar, but may be separated by the wide, flattened vas deferens possessed by the former species.

4. *Oxyloma retusa* is the only known species of Succineidae in Kansas that possesses a small appendix on the distal end of the penis and an epiphallus completely enclosed by the penial sheath.

5. The two species of *Quickella* lack a penial sheath and possess a large appendix which equals, or exceeds, the size of the penis. *Quickella wandae* is distinguished from *Q. vagans* by the long outgrowth from the distal end of the appendix that is present in the former species.

6. *S. pseudavara* is reported for the first time to occur in Kansas. It was found in four counties within the state. Additional collecting will be necessary to determine the abundance and distribution of this species.

7. *S. vaginacantorta* was collected only in Meade County, where it lived in association with *Q. vagans*. The former species has been reported in eastern Kansas.

8. *S. ovalis* barely enters the northeast corner of Kansas, occurring in Doniphan County.

9. *S. concordialis* is exceeded in abundance of individuals only by *Q. vagans*. The first species is distinctive in the living state by the intensely pigmented mantle and foot.

10. *Oxyloma retusa* occurs in Atchison and Doniphan counties, in northeastern Kansas. An *Oxyloma* has been reported from Meade County, but my search there failed to uncover it. Comparison of shells of *Oxyloma* from Meade, Atchison, and Doniphan counties suggests that *O. retusa* is the only species of *Oxyloma* occurring in Kansas.

11. *S. avara*, *S. grosvenori*, and *S. stretchiana* have been reported from Kansas by other workers, but I have not found these species and suspect that the specimens so identified were *Q. vagans*, or some other one of the species reported in the present account.

12. *Q. wandae* is known to occur in various counties in eastern Kansas. Only one specimen was collected in my study, from Franklin County.

13. The Family Succineidae seems adaptable to various ecological conditions. Several of the species have been found to inhabit wet situations and also dryer habitats.

14. Three kinds of parasites have been observed to infest the Succineidae in Kansas: a stage in the life cycle of a trematode (presumably *Leucochloridium*) in *Succinea ovalis*; a fly larva, apparently the first instar stage, in *S. concordialis* and in *Quickella vagans*; and a nematode, often infesting a large percentage of specimens from a single population, in *Q. vagans*.

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GUIDE TO TERMS USED IN FIGURES

apl, accessory plate	p, penis
ag, albumin gland	pg, prostate gland
ap, appendix	pr, penial retractor muscle
ce, cutting edge	ps, penial sheath
ep, epiphallus	r, ribs
ex, extension of appendix	sr, seminal receptacle
fs, fertilization sac	srd, duct of seminal receptacle
ga, genital atrium	sv, seminal vesicles
hd, hermaphrodite duct	tva, torsion in vagina
hg, hermaphrodite gland	va, vagina
od, oviduct	vd, vas deferens

PLATE I

EXPLANATION OF FIGURES

Dorsal and ventral views of shells shown in all figures

FIG. A—*Quickella wandae* Webb, No. 10274, April 8, 1956, 7 mi. N Ottawa, Franklin County, Kansas.

FIG. B—*Succinea ovalis* Say, No. 10265, April 22, 1956, $\frac{7}{10}$ mi. N White Cloud, Doniphan County, Kansas.

FIG. C—*Succinea vaginacontorta* Lee, No. 10266, June 3, 1956, Meade County State Park, Meade County, Kansas.

FIG. D—*Succinea pseudavara* Webb, No. 10268, June 3, 1956, Cimarron, Gray County, Kansas.

FIG. E—*Quickella vagans* (Pilsbry), No. 10273, July 28, 1955, Lone Star Lake, Douglas County, Kansas.

FIG. F—*Succinea concordialis* Gould, No. 10270, May 16, 1956, K. U. Natural History Reservation, 4 mi. N, $1\frac{1}{2}$ mi. E Lawrence, Douglas County, Kansas.

FIG. G—*Oxyloma retusa* (Lea), No. 10277, May 11, 1956, $1\frac{1}{2}$ mi. S Muscotah, Atchison County, Kansas.

FIG. H—*Oxyloma retusa* (Lea), No. 10276, September 4, 1955, $\frac{9}{10}$ mi. N Iowa Point, Doniphan County, Kansas.

FIG. I—*Succinea concordialis* Gould, No. 10271, June 5, 1956, 6 mi. W Altamont, Labette County, Kansas.

FIG. J—*Quickella vagans* (Pilsbry), No. 10272, June 12, 1956, $2\frac{3}{5}$ mi. W Burlingame, Osage County, Kansas.

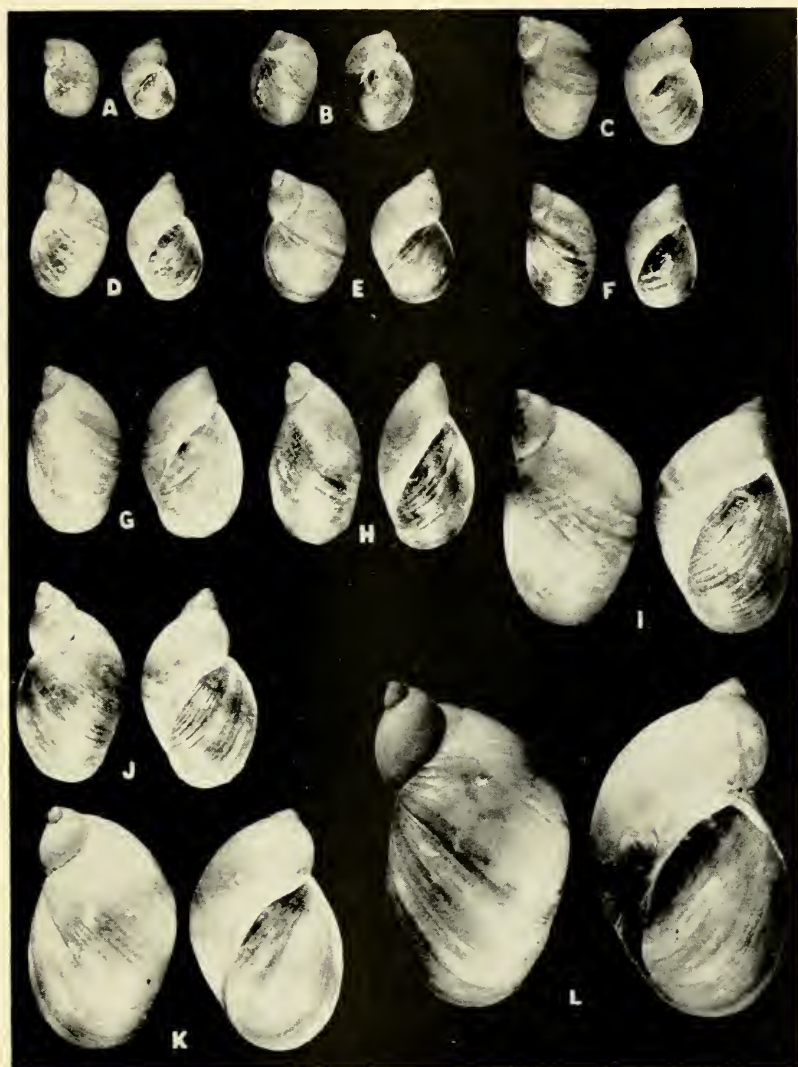
FIG. K—*Succinea ovalis* Say, No. 10265, April 22, 1956, $\frac{1}{2}$ mi. N White Cloud, Doniphan County, Kansas.

FIG. L—*Succinea ovalis* Say, No. 10264, April 9, 1955, $\frac{1}{2}$ mi. N White Cloud, Doniphan County, Kansas.

All figures approximately $\times 2$

Catalogue numbers are of the Mollusk Collection, University of Kansas Museum of Natural History.

PLATE I



FIGURES 2-4

FIG. 2. Genitalia of *Succinea ovalis* Say, K. U. 10264, April 9, 1955, $\frac{1}{2}$ mi. N White Cloud, Doniphan County, Kansas.

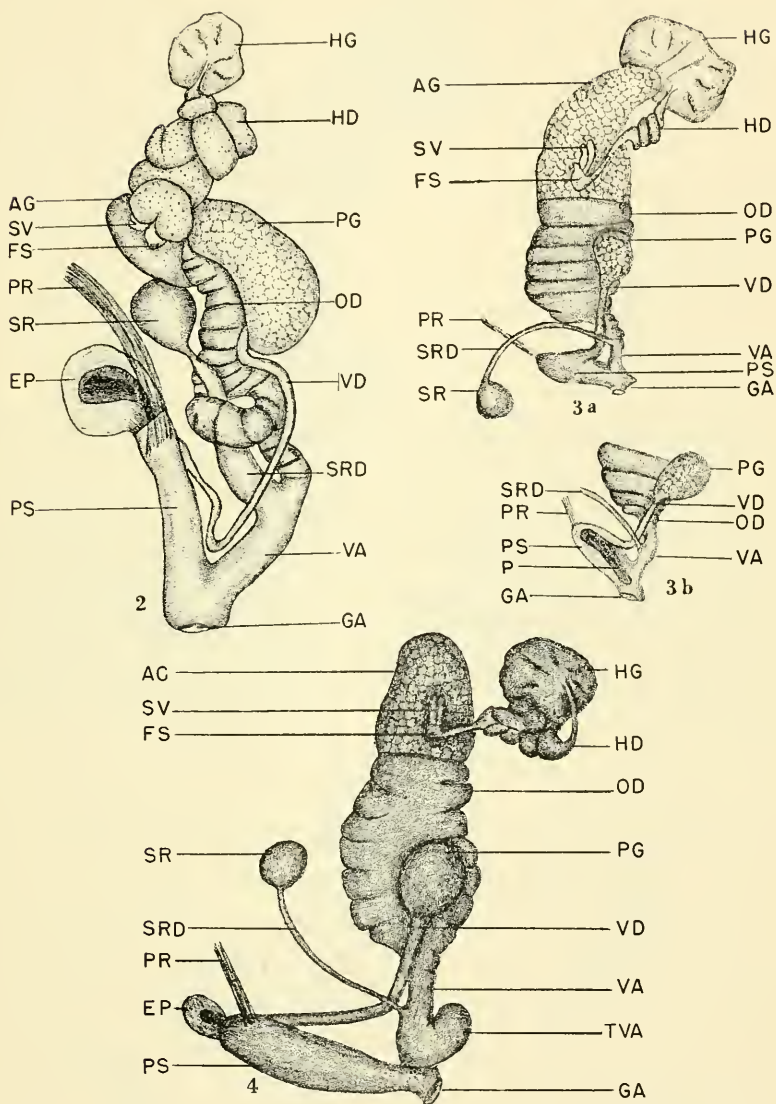
FIG. 3. Genitalia of *Succinea concordialis* Gould, K. U. 10327, June 2, 1956, St. Francis, Cheyenne County, Kansas.

a, complete genitalia.

b, drawing to show penis as it appear within the sheath.

FIG. 4. Genitalia of *Succinea vaginacontorta* Lee, K. U. 10266, June 3, 1956, Meade County State Park, Meade County, Kansas.

FIGURES 2-4



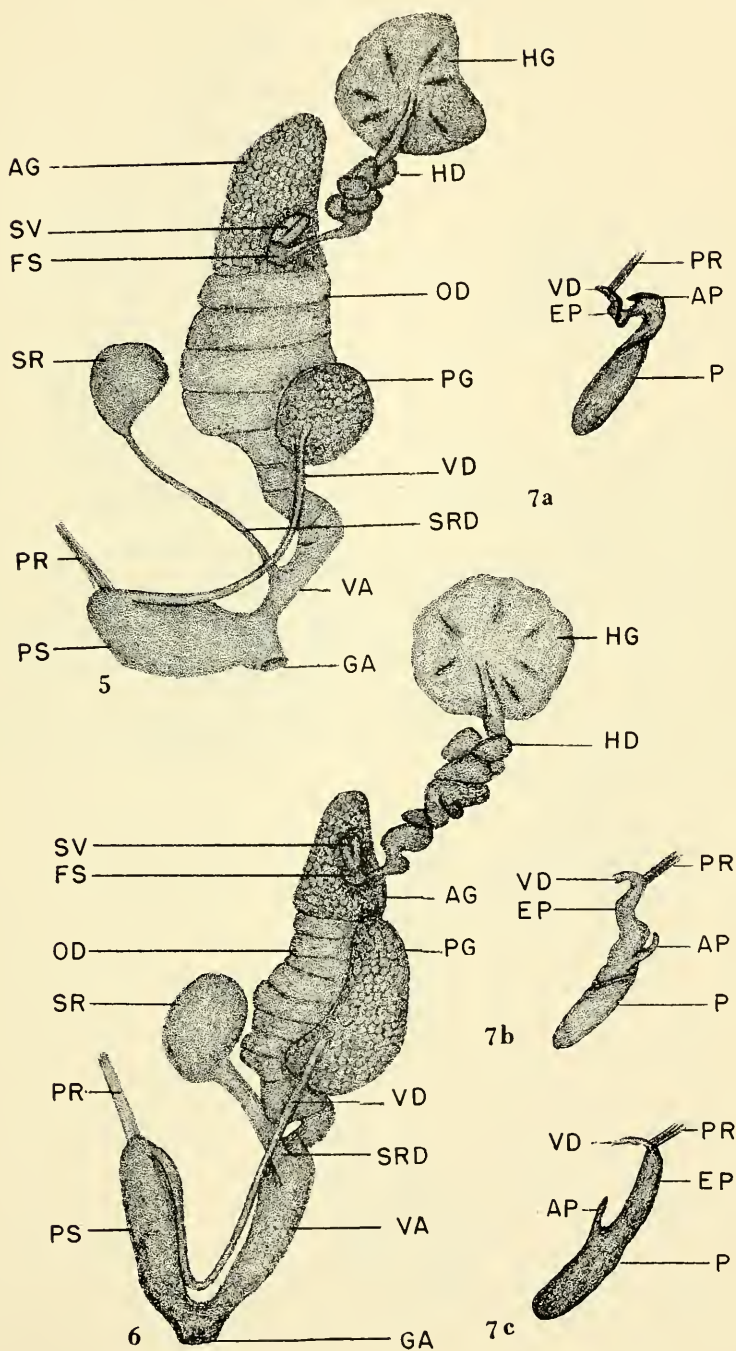
FIGURES 5-7

FIG. 5. Genitalia of *Succinea pseudavara* Webb, K. U. 10334, June 4, 1956, 4 mi. W Medicine Lodge, Barber County, Kansas.

FIG. 6. Genitalia of *Oxyloma retusa* (Lea), K. U. 10285, July 14, 1955, 1½ mi. S Muscotah, Atchison County, Kansas.

FIG. 7. Drawings of the penes and appendices of three specimens of *Oxyloma retusa* from one population, to show the variability in the appendix. Sheath of penis not shown. Note that the degree of coiling of epiphallus seemingly influences the position of the appendix. In a and b, the penis is coiled in a half-turn. In c, the straightening of the epiphallus has uncoiled the penis. The appendices shown in b and c represent about the maximum size attained by the structure. The appendix in a is more nearly typical, although many specimens of *Oxyloma retusa* possess smaller appendices than is shown here.

FIGURES 5-7



FIGURES 8-10

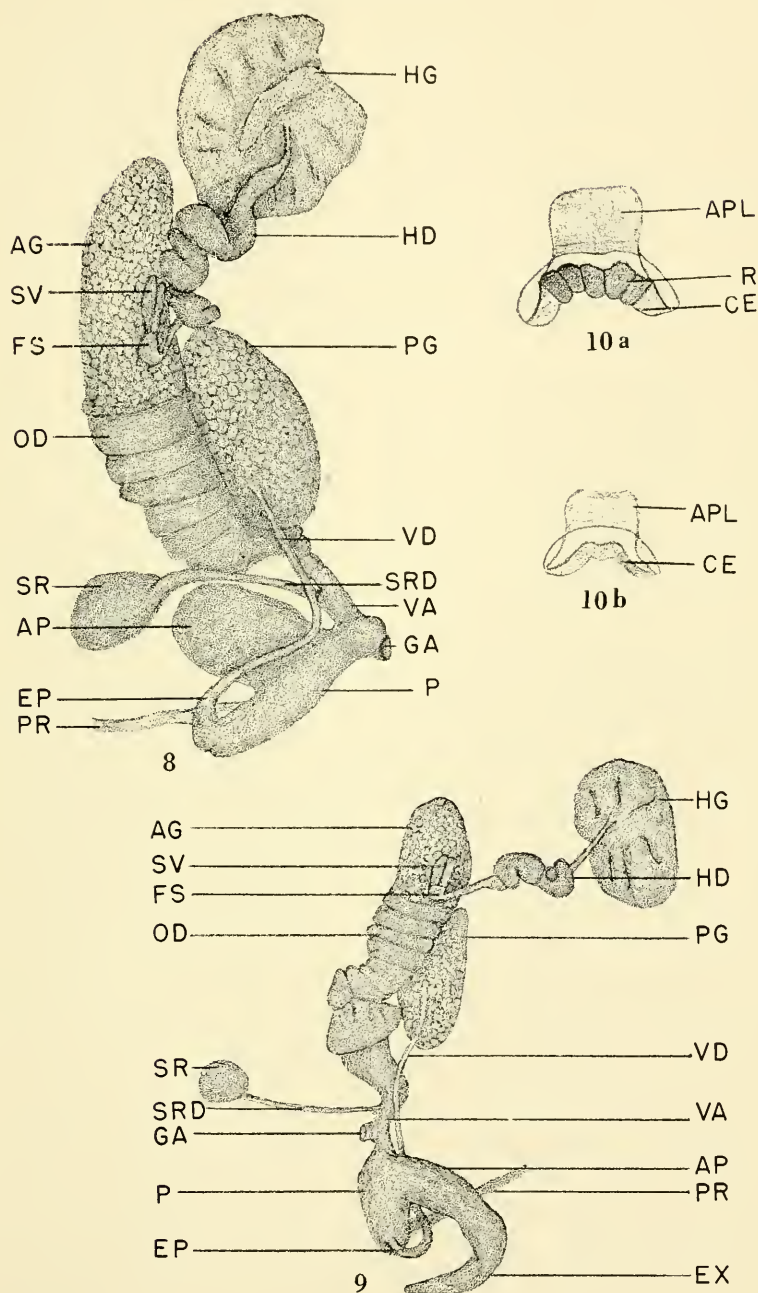
FIG. 8. Genitalia of *Quickella vagans* (Pilsbry), K. U. 10272, June 12, 1956, 2 $\frac{3}{4}$ mi. W Burlingame, Osage County, Kansas.

FIG. 9. Genitalia of *Quickella wandae* Webb, K. U. 10274, April 8, 1956, 7 mi. N Ottawa, Franklin County, Kansas.

Note: the penis and appendix have been twisted approximately 180 degrees in this drawing to show structures more advantageously. The normal position of these organs would be about the same as shown in Fig. 8.

FIG. 10. a, jaw of *Succinea ovalis* showing ribs on the anterior surface of the cutting edge. This is the only species of the Succineidae in Kansas possessing ribs. b, jaw of *Succinea concordialis*. The accessory plate (apl) shown in Figs. 10a and 10b is present on the jaws of all species of Succineidae and is a diagnostic feature of the family. Camera lucida drawings; figures a and b are drawn to same scale ($\times 40$).

FIGURES 8-10





26-8050

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